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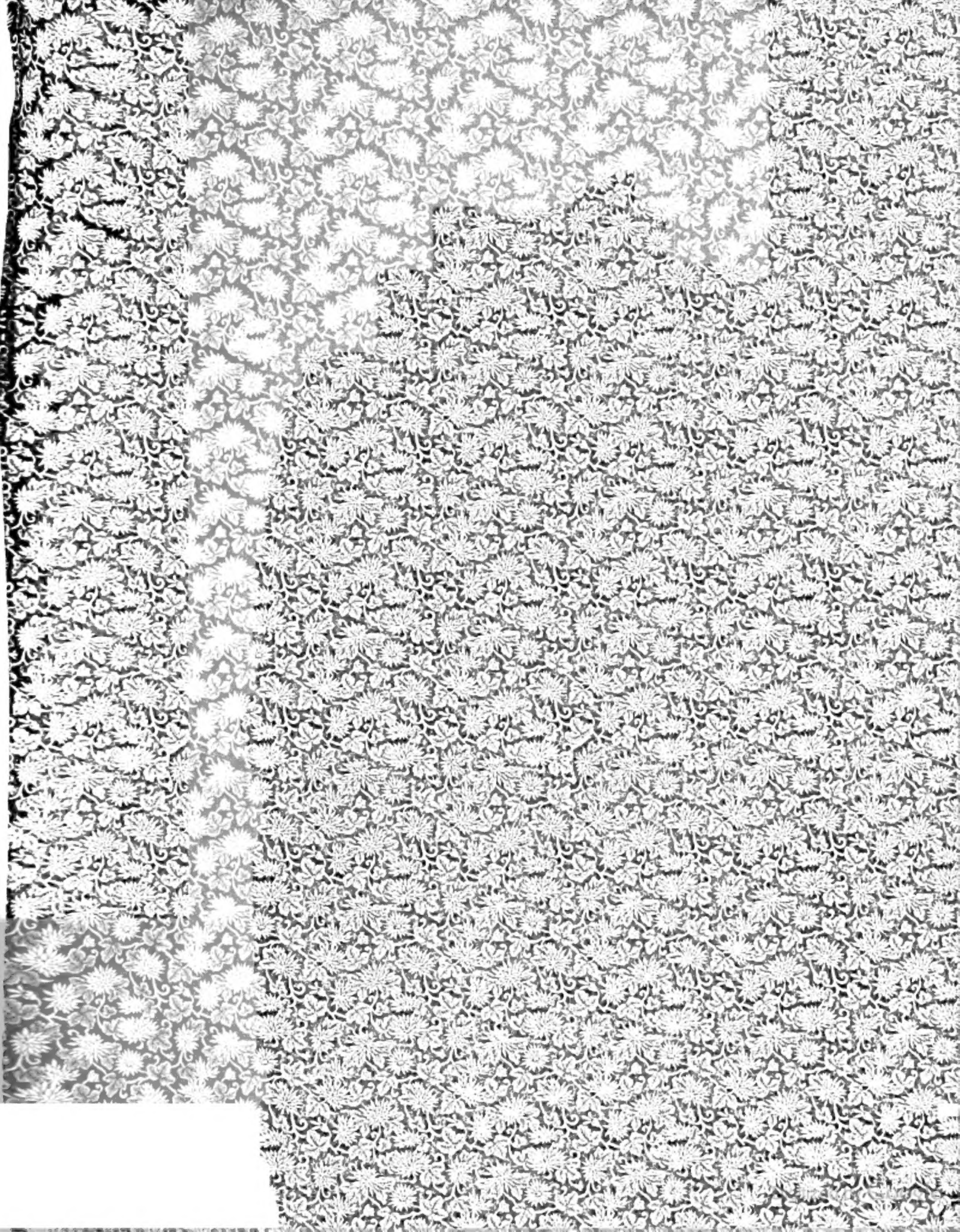
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THE  
TRANSACTIONS  
OF  
THE LINNEAN SOCIETY  
OF  
LONDON.

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SECOND SERIES.—VOLUME VIII.  
ZOOLOGY.

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TRANSACTIONS  
OF  
THE LINNEAN SOCIETY.

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I. *On a Collection of Brachyura from Torres Straits.* By W. T. CALMAN, D.Sc.,  
University College, Dundee. (Communicated by Prof. D'ARCY W. THOMPSON, C.B.,  
F.L.S.)

(Plates 1-3.)

Read 16th November, 1899.

INTRODUCTORY.

THIS paper deals with the Brachyurous Crustacea collected by Prof. A. C. Haddon during his first expedition to Torres Straits in 1888. The collection comprises about 87 species, three of which are described as new. Owing probably to the fact that attention was given to collecting the smaller and less conspicuous forms, a number of interesting and little-known species were obtained, some of which I have redescribed and figured. From the same cause, however, the determination of many of the specimens proved to be a matter of no little difficulty, and the identification of one or two of the more obscure species is at best provisional.

Of the three species here described as new, *Cryptocnemus Haddoni* belongs to a genus hitherto comprising only four species, all of which are known only from single specimens. *Pilumnus cristipes* is apparently very distinct from any known species, and its title to inclusion in the extensive genus *Pilumnus* may perhaps be disputed. *Lambrus confragosus* belongs to a genus already overburdened with species, but, so far as the means at my disposal enable me to judge, it seems to deserve the distinction of a specific name.

Among the species already known, concerning which I am able to furnish fresh details, the most interesting is the parasitic *Hapalocarcinus marsupialis*. Briefly described forty years ago by Stimpson, it appears to have escaped re-examination by carcinologists, though the curious gall-like growths to which it gives rise on corals are well known.

The occurrence of the three known Indo-Pacific species of *Palicus* (*Cymopolia*), two of which have been recorded hitherto only from widely distant localities, has afforded an opportunity for a detailed examination of their distinctive characters.

In the case of certain species described by Adams and White and by Miers, I have been able, from an examination of the type specimens in the British Museum (Natural History), to supplement the original accounts and to make one or two alterations in the matter of nomenclature.

I am much indebted to Prof. F. Jeffrey Bell and to Mr. R. I. Pocock for their courtesy and kindness in facilitating my work among the collections under their charge. My thanks are also due to Prof. E. L. Bouvier and Dr. J. G. de Man for giving me information and advice on various points, and to Dr. Chas. Chilton for the loan of literature relating to Australasian Crustacea\*.

As regards nomenclature and classification, I have followed, where possible, the important work of Dr. A. Alcock, 'Materials for a Carcinological Fauna of India,' now in course of publication. The extensive collections upon which his revision of the Indian species is based, and the exhaustive way in which the bibliography of the subject is treated, render this work indispensable for the student of the Indo-Pacific Crustacea.

#### List of the Species.

##### Tribe CYCLOMETOPA.

##### Family XANTHIDÆ.

- \**Carpilius convexus* (Forsk.).
- Carpilodes* sp.
- Liomera cinctimana* (White).
- \**Atergatis floridus* (L.).
- \**Lophactæa granulosa* (Rüpp.).
- \**Lophozozymus octodentatus* (M.-E.).
- *dodone* (Herbst).
- \**Xantho* (*Leptodius*) *exaratus* (M.-E.).
- \**Etisus lævimanus*, Rand.
- \**Etisodes frontalis*, Dana.
- \*— *electra* (Herbst).
- \**Actæa Rüppellii*, Krauss.
- \*— *calculosa* (M.-E.).
- *granulata*, var. *carcharias*, White.
- *Peronii*, var. *squamosa*, Hend. (?).
- \*— *hystrix*, Miers.
- Xanthodes Lamarckii* (M.-E.).

- \**Chlorodius niger* (Forsk.).
- \**Phymodius unguatus* (M.-E.).
- *sculptus* (A. M.-E.).
- Chlorodopsis melanodactylus*, A. M.-E.
- *spinipes*, A. M.-E.
- Cymo Andreossyi* (Aud.).
- *melanodactylus*, De Haan.
- \**Ozius guttatus* (M.-E.).
- Pseudozius dispar*, Dana.
- \**Pilumnus cursor*, A. M.-E.
- \*— *pulcher*, Miers.
- \*— *seminudus*, Miers.
- \*— *lanatus* (Latr. ?), Miers.
- *longicornis*, Hilg., var.
- *cristipes*, n. sp.
- \**Actumnus setifer* (De Haan).
- Trapezia ferruginea*, var. *areolata*, Dana.
- \*— *cymodoce* (Herbst).
- Tetralia glaberrima* (Herbst).

\* Since this paper was read I have been enabled, by the kindness of Mr. T. R. R. Stebbing, to consult Paulson's little-known work on the Crustacea of the Red Sea. Prof. Walker, of this College, has been good enough to translate for me several passages to which reference will be made.

## Family PORTUNIDÆ.

- Lissocarcinus orbicularis*, Dana.  
*Caphyra rotundifrons*, A. M.-E.  
 \**Neptunus sanguinolentus* (Herbst).  
 \*—— *pelagicus* (L.).  
 \*—— (*Achelous*) *granulatus* (M.-E.).  
 \*—— (——) ——, var. *unispinosus*, Miers.  
 \**Thalamita prymna* (Herbst).  
 \*—— *adinetæ* (Herbst).  
 \*—— *sima*, M.-E.

## Family CANCRIDÆ.

- \**Kraussia nitida*, Stimpson.

## Tribe CATOMETOPA.

## Family GRAPSIDÆ.

- \**Metopograpsus messor* (Forsk.).  
 \**Varuna litterata* (Fabr.).

## Family OCYPODIDÆ.

- \**Ocypoda ceratophthalma* (Pallas).  
*Uca* (= *Gelasimus*) *tetragonon* (Herbst).  
*Ceratoplax* sp.

## Tribe OXYSTOMA.

## Family CALAPPIDÆ.

- \**Calappa hepatica* (L.).

## Family LEUCOSIIDÆ.

- Cryptocnemus Haddoni*, n. sp.  
 \**Oreophorus frontalis*, Miers.  
 \**Myra fugax* (Fabr.).  
 \*—— *australis*, Hasw. (?).  
 \**Leucosia longifrons*, var. *pulcherrima*, Miers.  
 \*—— *Haswelli*, Miers.  
*Pseudophilyra tridentata*, Miers.  
*Arcania gracilipes*, Bell (?).

## Family DORIPPIDÆ (?).

- \**Palicus Jukesii* (White).  
 —— *Whitei* (Miers).  
 —— *serripes* (Alcock & Anderson).

## Tribe OXYRHYNCHA.

## Family MAIIDÆ.

- \**Acheus affinis*, Miers.  
 \**Paratymolus sexspinosus*, Miers.  
 \**Oncinopus aranea*, De Haan.  
 \**Xenocarcinus tuberculatus*, White.  
 \**Huenia proteus*, De Haan.  
 \**Menathius monoceros*, Latr.  
*Hyastenus spinosus*, A. M.-E.  
 \*—— *oryx*, A. M.-E.  
 \*—— *convexus*, Miers.  
 —— *verrucosipes* (Adams & White).  
 —— *Brockii*, De Man.  
 \**Nasia serpulifera* (Guér.).  
 \*—— *taurus*, Pocock.  
*Tylocarcinus styx* (Herbst).  
 \**Paramithrax* (*Chlorinoides*) *Coppingeri*, Hasw.  
 \*—— (——) *aculeatus* (M.-E.).  
 \**Schizophrys aspera* (M.-E.).  
*Cyclax suborbicularis* (Stimpson).  
 \**Pseudomicippa varians*, Miers.  
 \**Micippa philyra* (Herbst).  
 \**Tiarinia angusta*, Dana.

## Family PARTHENOPIDÆ. [var. ?]

- \**Lambrus* (*Aulacolambrus*) *hoplonotus*, Ad. & Wh.,  
 \*—— (*Parthenolambrus*) *calappoides*, Ad. & Wh.  
 —— (——) *confragusus*, n. sp.

## Incertæ sedis.

## Family HALALOCARCINIDÆ (nom. nov.).

- Hapalocarcinus marsupialis*, Stimpson.

In the above list I have marked with an asterisk those species which have been already recorded from the North or North-east of Australia. Of the species not so recorded the majority are known to have a wide distribution within the Indo-Pacific region, and the few cases where the range of a species is considerably extended (e. g., *Palicus Whitei*) merely help to emphasize the uniformity of the crustacean fauna, whose range is coterminous with that of the coral-reefs over this extensive area.



**CARPILIUS CONVEXUS (Forsk.).**

*Carpilius convexus*, H. Milne-Edwards, Hist. Nat. Crust. i. p. 382, pl. xvi. figs. 9-10; Alcock, Journ. Asiatic Soc. Bengal, lxvii. (2) p. 80 (1898).

Three females and two males. One labelled "Found within hollow in *Tubipora*."

*Locality*. "Mer."

**CARPILODES sp.**

A number of very small specimens belonging to this genus do not agree satisfactorily with any of the described species, but in the absence of a larger series for comparison I do not venture to describe them as new. They are identical with certain small specimens in the British Museum determined as *C. rugatus*, Latr., but differ from larger specimens of that species and from the figure given by A. Milne-Edwards (N. Arch. Mus. Paris, i. pl. xii. figs. 3, 3 a-b) in the fact that the lobulations on the surface of the carapace, and especially on the branchial regions, are more numerous and do not have the regularly transverse direction so marked in *C. rugatus*.

The *C. cariosus* of Alcock (Journ. Asiatic Soc. Bengal, lxvii. (2) 1898, p. 86, and Illustr. Zool. 'Investigator,' Crust. pl. xxxvi. fig. 7, 1899) \* resembles our specimens rather closely; but in that species the carapace is not quite so broad, the antero-lateral borders less convex, and the lobules on the lateral regions of the carapace are arranged in a slightly different manner.

*Locality*. "Murray Island, 15-30 fms."

**LIOMERA CINCTIMANA (White).**

*Carpilius cinctimanus*, White, in Jukes's Voy. 'Fly,' ii. Appendix, p. 336, pl. ii. fig. 3 (1847); Adams & White, Voy. 'Samarang,' Crust. p. 37, pl. vii. fig. 4.

*Liomera lata*, Dana, U.S. Expl. Exp., Crust. i. p. 161, pl. vii. figs. 6 a-d.

*L. cinctimana*, Dana, op. cit. p. 161.

*L. lata* and *L. cinctimana*, A. Milne-Edwards, N. Arch. Mus. Paris, i. pp. 219-220 (1865).

*L. cinctimana*, A. Milne-Edwards, N. Arch. Mus. Paris, ix. p. 176, pl. v. fig. 4 (1873).

*Carpilodes cinctimanus*, Miers, Ann. & Mag. Nat. Hist. (5) v. p. 234 (1880); Henderson, Tr. Linn. Soc., (2) Zool. v. p. 354 (1893).

*L. cinctimana*, Ortmann, Zool. Jahrb. Syst. vii. p. 450 (1893); Alcock, Journ. Asiatic Soc. Bengal, lxvii. (2) p. 88 (1898).

Two male and two female specimens.

*Locality*. "Murray Island."

*Distribution*. Zanzibar to Tahiti.

The synonymy of this species and of the genus of which it is the type give striking evidence of the intangible nature of the characters on which we are forced to rely in the classification of the Xanthoid crabs. As defined by Dana, *Liomera* is stated to resemble *Carpilius* in the disposition of the antennæ (that is to say, the basal antennal joint enters into the inner orbital hiatus), and the genus is separated from *Carpilodes* only by the fact that the fingers are said to be sharp-pointed instead of spoon-shaped at the tip.

\* Cf. also Nobili, Ann. Mus. Genova, (2) xx. p. 256 (1899).

A. Milne-Edwards in his monograph of the Cancridæ (*l. c.* 1865) abandoned the use of the character drawn from the shape of the finger-tips as a generic distinction, but he retained the genus *Liomera*, placing it in the group of genera having the basal antennal joint "s'unissant seulement au front par son angle interne," and separating it thus from *Carpilodes* by a character in direct contradiction to the original definition of the genus. Miers in 1880 (*l. c.*) referred our species to *Carpilodes*, accepting that genus in Milne-Edwards's sense as having the basal joint of the antenna "produced along the exterior margin of the infero-lateral frontal process so as to enter partly within the interior orbital hiatus" (Chall. Rep., Brachyura, p. 133, 1886). Although thus deprived of its type species, the genus *Liomera* was retained by Miers, who defines it (Rep. Voy. 'Alert,' Crust. p. 528) very much as Milne-Edwards had done, and refers to it certain species which he later included (Chall. Rep. p. 125) in the genus *Xantho*. Ortmann and Alcock return to Milne-Edwards's position, including this species in *Liomera* and defining it as having the basal antennal joint not entering the orbital hiatus, and the first-named author gives a figure of *L. cinctimana* to illustrate this very point. It will thus be seen that of the authors who have examined this species Dana and Miers regard the basal antennal joint as entering the inner orbital hiatus, while Milne-Edwards, Ortmann, and Alcock state explicitly that it does not. As a matter of fact, *Liomera* occupies in this respect an intermediate position between two extremes, which are connected by a continuous series of gradations. On the one hand, we have forms where the basal joint lies nearly longitudinally and meets the posterior process of the front at its tip, so that the short line of junction between the two is transverse to the axis of the joint; on the other hand, we may have the basal joint lying very obliquely to the axis of the body, meeting the frontal process with its inner edge, so that the prolonged line of junction is approximately parallel to the axis of the joint, which thus lies more or less completely in the hiatus between the frontal process and the lower wall of the orbit. In the present species, however, the short trapezoidal basal joint meets the frontal process at its tip, but the short line of junction between the two is obliquely placed with reference to the long axis of the joint, so that a small portion of the latter may be regarded as lying in the orbital hiatus between the frontal process and the suborbital wall. Moreover, some individual variation in this respect is observed when a series of specimens is examined, and, if we may judge by the analogous case of *Actea calculosa* referred to below, it would seem that this character is liable to change with the growth of the individual.

#### ATERGATIS FLORIDUS (L.).

*Atergatis floridus*, Alcock, Journ. Asiatic Soc. Bengal, lxvii. (2) p. 98 (1898).

Two small specimens of this widely distributed and common Indo-Pacific species. The carapace of the larger is 10 mm. long and 16 mm. broad, the relative breadth being somewhat greater than in larger specimens.

*Locality.* "Murray Island, reef."

**LOPHACTÆA GRANULOSA (Rüpp.).**

*Cancer limbatus*, H. Milne-Edwards, Hist. Nat. Crust. i. p. 377, pl. xvi. figs. 1-3.

*Lophactæa granulosa*, A. Milne-Edwards, N. Arch. Mus. Paris, i. p. 247; Alcock, Journ. Asiatic Soc. Bengal, lxvii. (2) p. 101 (1898).

A female specimen.

*Locality.* "Torres Straits."

**LOPHOZOZYMUS OCTODENTATUS (Milne-Edwards).**

*Xantho octodentatus*, H. Milne-Edwards, Hist. Nat. Crust. i. p. 398.

*Lophozozymus octodentatus*, Haswell, Cat. Austr. Crust. p. 58.

*L. epheliticus* (L.), Miers, Crust. Voy. 'Alert,' p. 207; De Man, Zool. Jahrb. Syst. viii. p. 518.

*L. octodentatus*, Alcock, Journ. Asiatic Soc. Bengal, lxvii. (2) p. 106 (1898).

Three male and three female specimens. The largest, a male, has the carapace 75 mm. broad, and in it, as in the other smaller specimens of both sexes, the chelæ are about equal in size. The difference between the sexes in the prominence of the last two pairs of antero-lateral teeth noted by De Man (*l. c.* p. 519) does not hold good for our specimens.

*Locality.* "Fringing reef, Mabuiag."

**LOPHOZOZYMUS DODONE (Herbst).**

*Lophozozymus dodone* (Hbst.), De Man, Arch. Naturg. liii. (1) p. 270, pl. x. figs. 2, 2 a (1887); Alcock, Journ. Asiatic Soc. Bengal, lxvii. (2) p. 108 (1898).

Two female specimens, about 13 mm. broad, agreeing perfectly with the figures and short description given by De Man. The grooves on the outer and inner surfaces of the dactylus of the chelipeds are very broad, and the upper margin between them is reduced to a thin sharp crest. De Man notes that these grooves are deeper in young individuals.

*Locality.* "Channels between reefs, Mer."

*Distribution.* Mozambique to Tahiti.

**XANTHO (LEPTODIUS) EXARATUS (Milne-Edwards).**

*Chlorodius exaratus*, H. Milne-Edwards, Hist. Nat. Crust. i. p. 402.

*Leptodius exaratus*, A. Milne-Edwards, N. Arch. Mus. Paris, ix. p. 222 (1873); De Man, Arch. Naturg. lii. (1) p. 285 (1887).

*Xantho (Leptodius) exaratus*, Alcock, Journ. Asiatic Soc. Bengal, lxvii. (2) p. 118 (1898).

A single small female specimen of this common and variable species. It appears to differ from the typical form, as described by the authors quoted above, only in the fact that the wrist and hand of the chelipeds are rugose above and the outer face of the hand is granulated.

*Locality.* "Cockburn group (N. Queensland), shore."



**ETISUS LEVIMANUS, Rand.**

*Etisus levimanus*, Rand., Dana, U.S. Expl. Exp., Crust. i. p. 185, pl. x. fig. 1; Alcock, Journ. Asiatic Soc. Bengal, lxvii. (2) p. 131 (1898).

A single small specimen (17.5 mm. long) agreeing in general shape and proportions of carapace with the still smaller specimens figured by Dana (*l. c.* fig. 1, *f*), the breadth-ratio of the carapace being the same (1.46) as that given by him. In full-grown specimens the carapace is much more transverse, the breadth-ratio being about 1.6.

*Locality.* "Fringing reef, Mabuiag."

**ETISODES FRONTALIS, Dana.**

*Etisodes frontalis*, Dana, U.S. Expl. Exp., Crust. i. p. 187, pl. ix. fig. 3; De Man, Notes Leyden Mus. xii. p. 8, pl. 1. fig. 2.

Our two specimens (about 11.5 mm. long by 17.25 mm. broad) agree more closely with De Man's figure than with Dana's, which is taken from a very small specimen only 8 mm. broad. The slight emargination of the frontal lobes is even less marked than in De Man's figure, these lobes being nearly transversely truncate. The posterior teeth of the antero-lateral margin are rather less spiniform, and some other slight differences are to be gathered from De Man's detailed description.

*Locality.* "Fringing reef, Mabuiag."

**ETISODES ELECTRA (Herbst).**

*Etisodes sculptilis*, Heller, SB. Ak. Wien, xliii. p. 333 (1861); A. Milne-Edwards, N. Arch. Mus. Paris, ix. p. 236, pl. ix. fig. 2 (1873).

*E. electra* (Hbst.), De Man, Arch. Naturg. liii. (1) p. 290 (1887).

Two specimens, agreeing well with Heller's description and Milne-Edwards's figure. The larger, a female, measures 7 mm. in length by 10 mm. in breadth (breadth-ratio 1.42), and is thus somewhat broader than is indicated by either of the authors named, whose measurements give the breadth-ratio as 1.36 and 1.38 respectively. The smaller specimen is a male 4 mm. long by 5.25 mm. broad, giving a ratio of about 1.31.

*Locality.* "Murray Island, reef."

**ACTÆA RÜPPELLII, Krauss.**

*Actæa Rüppellii* (Kr.), De Man, Zool. Jahrb. Syst. viii. p. 499 (1895); Alcock, Journ. Asiatic Soc. Bengal, lxvii. (2) p. 144 (1898).

Our specimens agree in most points with the description of this species as given by De Man (*l. c.* and earlier papers there referred to). They show some variation in the hairiness of the body and in the prominence of the regional divisions of the carapace. One specimen, considerably larger than the others, differs from them in the greater length of the hairs on the carapace and in the scantiness of the short down which in the other specimens covers the carapace below the long hairs. In this specimen the finger-tips are slightly excavate. All our specimens can be matched from the series referred

to *A. Rüppellii* in the British Museum collections, but in none of the latter are the hairs quite so long as in our largest individual.

*Localities.* "Murray Island"; "Thursday Island, fringing reef and shore"; "Albany Passage, 10 fath."

*ACTÆA CALCULOSA* (Milne-Edwards).

*Cancer calculosus*, H. Milne-Edwards, Hist. Nat. Crust. i. p. 378 (1834).

*Actæa calculosa*, A. Milne-Edwards, N. Arch. Mus. Paris, i. p. 276, pl. xviii. fig. 3 (1865); Haswell, Cat. Austr. Crust. p. 45 (1882).

*Euzanthus tuberculosus*, Miers, Crust. 'Alert,' p. 205, p. xix. fig. A (1884).

*Actæa calculosa*, Henderson, Tr. Linn. Soc. London, (2) Zool. v. p. 356 (1893); Alcock, Journ. Asiatic Soc. Bengal, lxxvii. (2) p. 152 (1898).

Five specimens of this species are in the collection. Prof. E. L. Bouvier has very kindly taken the trouble to compare one of our specimens, sent to him for the purpose, with the original type specimen of H. Milne-Edwards's *Cancer calculosus* in the Paris Museum. He writes as follows:—

"J'ai comparé minutieusement votre Crabe avec le type d'*Actæa calculosa*, Edw. Il appartient évidemment à la même espèce. Les tubercules du test y sont beaucoup plus saillants, mais ils sont partout disposés dans le même ordre et sont entourés aussi d'une auréole périphérique de punctuations. . . . je vous le repète, on ne saurait douter de l'identification."

The identification of our specimens being vouched for on such excellent authority, it may be useful to give in some detail their characters as compared with *Actæa granulata* (Aud.), since it appears that recent writers have not always successfully distinguished the two species.

The breadth-ratio of the carapace varies from 1.33 to 1.4 without apparent relation to the actual size. The three posterior lobes of the antero-lateral margin are prominent and well-defined, and in front of these the first lobe is represented by a single tubercle. In *Actæa granulata*\* the lobes are low, rounded, and indistinctly separated. The regions of the carapace are much more distinct in *A. calculosa*, being separated by rather deep grooves, which are in part smooth and free from granules. There is a marked and generally smooth groove parallel to the hinder margin of the carapace and separated from it by two or, in one case, three rows of granules. The posterior margin is defined at each end by a small spiniform tubercle which is not distinct in *A. granulata*. The cardiac area is of a rather different shape from that shown in the figure given by A. Milne-Edwards, being produced and much narrowed anteriorly. The tubercles on the surface of the carapace are rounded, smooth, and surrounded each by radiating punctations. On the posterior part of the carapace in some specimens they become depressed and confluent. In *A. granulata* the tubercles are more pointed and the radiating

\* I have used for comparison two specimens of *A. granulata* from Japan in the Museum of University College. These differ slightly from Savigny's figure (Descr. de l'Égypte, Crust. pl. vi. fig. 2) in the rougher appearance of the carapace, but they seem to agree in all essential points with this as well as with the descriptions of later writers.

punctations mark off more or less prominent accessory tubercles which surround the base of each large tubercle. The frontal lobes in *A. calculosa* are smooth or indistinctly granulated on the edge, while in *A. granulata* they are edged with pointed granules. In *A. calculosa* the outer surface of the hands bears smooth, bluntly conical tubercles arranged in longitudinal rows; in *A. granulata* the tubercles are lower, surrounded by prominent and pointed accessory tubercles, and the arrangement in rows is less regular. The walking-legs are covered with tubercles rounded at the tip, smooth, and larger in size than in *A. granulata*, where they are low, pointed, and more numerous. The merus joint of the last pair of legs is strongly serrate above, the serrations increasing in height towards the distal end, and its posterior face is nearly smooth. In *A. granulata* the serrations of the upper edge are small and irregular, and the posterior surface is covered with granulations. The sternum and abdomen, especially in the male, are smooth, with scattered punctations, while in *A. granulata* the same regions are usually much granulated, at least posteriorly.

In his report on the Crustacea collected by H.M.S. 'Alert,' Mr. Miers has described and figured, under the name of *Euxanthus tuberculosus*, a species which I believe, after examination of his type specimens, to be identical with the present. Mr. Miers writes, "As the basal antennal joint enters well within the inner orbital hiatus, this species must, I think, be referred to the genus *Euxanthus*." In his specific description the account of the basal antennal joint is qualified by the words "in the adult," and certainly the difference in this respect between the largest and the smallest of the specimens he was describing is conspicuous enough to have suggested a doubt as to the validity of a generic distinction resting on this point alone. As a matter of fact it is easy to find specimens both of the present species and of *A. granulata* in which the basal antennal joint enters quite as far into the orbital hiatus as in any but the largest of Miers's specimens\*. The individual which he figures, and from which his description is mainly drawn, is a large male, 23 mm. in length. The carapace is rather wider than in smaller specimens, the breadth-ratio being about 1.43, and the tuberculation of the carapace is very strongly developed. The smaller specimens associated with this by Mr. Miers, and obtained by the 'Alert' in the vicinity of Torres Straits, are all but identical with the specimens in the present collection from the same locality. Mr. Miers further states that the smaller specimens "have much the aspect of certain *Actææ*, e. g., *A. granulata* (Aud.) and *A. carcharias*, White; from both of which species they may be distinguished upon the most superficial examination by the smoothness of the sternum and post-abdomen." In spite of the emphasis of the last sentence, I find in the British Museum collections specimens determined by Mr. Miers as *A. granulata* (among others the one referred to in his 'Challenger' Report, p. 120) which resemble in every respect the smaller types of his "*Euxanthus tuberculosus*." The few specimens referred to *A. calculosa* in the British Museum collection are rather different in appearance from our Torres Straits specimens,

\* Paulson (whose work Mr. Miers had not seen) had already established a new genus *Euxanthodes* for the reception of *Actæa granulata* on account of the structure of its antennal region, which he figures ('Crustacea of the Red Sea' (Russian), Kiev, 1875, p. 33, pl. vi. figs. 3 & 3 a).

the tubercles on the carapace being very much depressed, confluent, and smooth. I believe, however, that they must be referred to the same species.

*Localities.* "Thursday Island"; "S. of Orman's reef, 5-7 fath."; "Channels between reefs, Mabuiag"; "Channels between reefs, Mer and Dara" (5 specimens).

*ACTÆA GRANULATA*, var. *CARCHARIAS* (White).

*Actæa carcharias*, White, Proc. Zool. Soc. London, 1847, p. 224; A. Milne-Edwards, N. Arch. Mus. Paris, i. p. 276 (1865).

A single female specimen, perhaps sterile, the abdomen appearing unusually narrow. It agrees perfectly with White's type specimen in the British Museum, save that the under surface is rather smoother. I have no doubt that Miers is right in regarding this as merely a variety of *A. granulata* (Chall. Rep., Brachyura, p. 122). The Japanese specimens of *A. granulata* referred to above show a tendency towards this variety in the rougher aspect of the carapace as compared with Savigny's figure.

*Locality.* "S. of Orman's reef."

*Distribution.* Swan River, W. Australia (*White*).

*ACTÆA PERONII*, var. *SQUAMOSA*, Henderson (?).

*Actæa Peronii*, var. *squamosa*, Henderson, Tr. Linn. Soc. London, (2) Zool. v. p. 357.

A male specimen, 10 mm. in length and 14 mm. in breadth. It differs much in appearance from the few specimens of *A. Peronii* (all of smaller size) available for comparison, but it agrees closely with the short description given by Prof. Henderson of his var. *squamosa*. The tubercles of the antero-lateral margin are replaced by sharp spines, of which there are five on each side behind the external orbital tooth. In the typical *A. Peronii* there are only four tubercles on the antero-lateral margin.

*Locality.* "Torres Straits."

*Distribution.* India (*Henderson*).

*ACTÆA HYSTRIX*, Miers.

*Actæa hystrix*, Miers, Rep. 'Challenger' Brachyura, p. 121, pl. xi. fig. 3.

Four female specimens having the following dimensions:—

Length.	Breadth.	Breadth-ratio.
4.5 mm.	5.5 mm.	1.22
5.0 "	6.5 "	1.3
5.5 "	7.5 "	1.36
7.0 "	10.0 "	1.43

The measurements given by Miers are:—

6.0 mm.	8.0 mm.	1.33
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Our smaller specimens agree very closely with the single type specimen. The measurements given above show a regular increase in the relative breadth of the carapace with increasing age. In the largest specimen the antero-lateral borders are more curved, the front is narrower, and the carapace departs from the hexagonal outline which it presents in the smaller specimens as in Miers's figure. The surface of the carapace is

more closely granulated than is shown in the figure, the granules being of different sizes, smooth and rounded on the posterior part of the carapace, and becoming spiniform in front and at the sides. The spinules on the hand are more thickly set and those on the legs are longer than in Miers's figure.

*Locality.* "Torres Straits."

With the above I may associate provisionally two specimens which I cannot identify with certainty. The smaller (length 5 mm., breadth 7 mm.) resembles somewhat closely the specimens of *A. hystrix*, differing chiefly in the blunter armature of the body and legs. The granules of the carapace are less closely packed and are rounded, not spiniform in any part; on the chelipeds they are conical, and on the legs they have the form of bluntly truncated spines. In the larger specimen (length 9 mm., breadth 12.5 mm.) the granules of the carapace are still more depressed and smoother, and the tubercles on the limbs are less prominent. These specimens differ from *Actæa nodulosa*, Ad. & White, in the much narrower carapace, the breadth-ratio of which is about 1.4 as compared with 1.56 in the last-named species. The *Chlorodius fragifer* of Adams and White, referred to *Actæodes* by Miers, is apparently a somewhat similar species, but the carapace is still narrower (breadth-ratio 1.19) than in our specimens and the lobes of the antero-lateral margins are indistinct and spined. I think it not improbable that a larger series would connect these specimens with *A. hystrix* and possibly with some of the older species.

#### XANTHODES LAMARCKII (Milne-Edwards).

*Xantho Lamarckii*, H. Milne-Edwards, Hist. Nat. Crust. i. p. 391.

*Xanthodes granosomanus*, Dana, U.S. Expl. Exp., Crust. i. p. 175, pl. viii. figs. 10 a-c.

*Xanthodes Lamarckii*, A. Milne-Edwards, N. Arch. Mus. Paris, ix. p. 200, pl. vii. fig. 3; De Man, Arch. Naturg. liii. (1) p. 263; Alcock, Journ. Asiatic Soc. Bengal, lxvii. (2) p. 157.

A male specimen, 10.5 mm. in length by 15.5 mm. in breadth. The carapace is relatively narrower than in other specimens of this species in the Museum of University College.

*Locality.* "Torres Straits."

#### CHLORODIUS NIGER (Forsk.).

*Chlorodius niger*, Alcock, Journ. Asiatic Soc. Bengal, lxvii. (2) p. 160 (1898).

Eleven specimens, four males and seven females, showing some variation in the relative prominence of the lobules on the carapace and in the acuteness of the antero-lateral teeth. Some of the specimens show very distinctly the spinulation of the upper edge of the merus of the ambulatory legs which De Man finds in the type specimens (Zool. Jahrb. Syst. viii. p. 520).

*Localities.* "Fringing reef and shore, Thursday Island"; "Reef, Wyer."

#### PHYMIDIUS UNGULATUS (Milne-Edwards).

*Chlorodius unguatus*, H. Milne-Edwards, Hist. Nat. Crust. i. p. 400, pl. xvi. figs. 5-8; Dana, U.S. Expl. Exp., Crust. i. p. 205, pl. xi. figs. 8 a-b.

*Phymodius unguatus*, A. Milne-Edwards, N. Arch. Mus. Paris, ix. p. 218; Miers, Rep. 'Chall.'



*Brachyura*, p. 139; Ortmann, *Zool. Jahrb. Syst.* vii. p. 464; De Man, *Zool. Jahrb. Syst.* vii. p. 524; Alcock, *Journ. Asiatic Soc. Bengal*, lxvii. (2) p. 162 (1898).

Three female specimens.

Ortmann (*l. c.*) unites Dana's *P. monticulosus* with this species, but Alcock (*l. c.*) retains it as distinct. The characters chosen by Alcock as diagnostic do not seem quite consistent with the descriptions of former writers and do not enable me to discriminate between the species in a series of eleven specimens from Samoa and Japan in our Museum. The three specimens in Prof. Haddon's collection agree with the original description of *P. monticulosus* in having the chelipeds "armed with very small pointed tubercles"; but as these tubercles beset the whole outer surface of the hand, the specimens would by Alcock's definition be referred to *P. unguatus*. As regards the sculpture of the carapace, I can observe no constant difference between these and specimens from Samoa, in which the chelipeds are distinctly of Alcock's *monticulosus*-type.

*Locality.* "Torres Straits."

#### PHYMODIUS SCULPTUS (A. Milne-Edwards).

*Chlorodius sculptus*, A. Milne-Edwards, *N. Arch. Mus. Paris*, ix. 1873, p. 217, pl. viii. fig. 4.

*Phymodius sculptus*, Alcock, *Journ. Asiatic Soc. Bengal*, lxvii. (2) p. 164 (1898).

Two male specimens, the larger measuring 10.5 mm. in length by 16.5 mm. in breadth. They agree very closely with the figures and descriptions quoted above.

*Locality.* "Torres Straits."

*Distribution.* Red Sea to Samoa.

#### CHLORODOPSIS MELANODACTYLUS, A. Milne-Edwards.

*Chlorodopsis melanodactylus*, A. Milne-Edwards, *N. Arch. Mus. Paris*, ix. p. 229, pl. viii. fig. 7 (1873).

Two male specimens, agreeing well with Milne-Edwards's description and figures, save that the hands, and especially the fingers, are rather longer and the tubercles on the fingers are more numerous. The series of specimens in the British Museum shows some variation in these respects, but in none are the hands so elongated as in our specimens.

*Locality.* "Murray Island, reef."

*Distribution.* New Caledonia.

#### CHLORODOPSIS SPINIPES (Heller).

*Pilodius spinipes*, Heller, *SB. Ak. Wien*, xliii. p. 340, pl. ii. fig. 22 (1861).

*Chlorodopsis spinipes*, A. Milne-Edwards, *N. Arch. Mus. Paris*, ix. p. 230, pl. viii. fig. 6 (1873);

De Man, *Arch. Naturg.* liii. (1) p. 282 (1887); Alcock, *Journ. As. Soc. Bengal*, lxvii. (2) p. 169 (1898).

A male and a female specimen are in the collection. De Man has given a redescription of the antero-lateral teeth, finding the descriptions of Heller and Milne-Edwards obscure. Heller's account, however, is quite applicable at least to the larger of the two specimens before me. He mentions (1) two teeth at the outer end of the upper and lower margins of the orbit respectively, enclosing between them a deep notch, the external orbital hiatus; (2) the three spiniform teeth of the antero-lateral margin;

(3) in front of the first of these latter, "zwei ähnlich gestaltete Zähnechen über und unter dem Rande unmittelbar hinter der Augenhöhle." The figure which he gives shows clearly that the upper tooth of the last-mentioned pair (3) is simply the most anterior of a row of spiniform tubercles running parallel to the antero-lateral margin on the upper surface of the carapace. In the figure this tooth is acute and much larger than the others; in our specimens it is much less prominent and less acute, but still considerably larger than the succeeding tubercles. It is directly over the "sub-hepatic" tubercle or tooth, which is evidently the second tooth of (3), and, looking at the carapace from the front or the side, the two are naturally associated as in Heller's description. Milne-Edwards's account is briefer, and does not mention the double extra-orbital spine. The row of tubercles parallel to the antero-lateral margin is described, and four antero-lateral teeth are counted, that which we have called "sub-hepatic" being reckoned as the first. The figure given by Milne-Edwards resembles very closely the larger of our two specimens. The smaller specimen differs in the fact that the sub-hepatic tooth (the first antero-lateral of Milne-Edwards) is nearly obsolete, being represented only by a minute granule. This seems to have been the case with the single specimen examined by De Man, who was thus unable to reconcile the apparently conflicting statements of Heller and Milne-Edwards.

*Locality.* "Murray Island, reef."

*Distribution.* Red Sea to New Caledonia.

#### CYMO ANDREOSSYI (Aud.).

*Cymo Andreossyi*, Dana, U.S. Expl. Exp., Crust. i. p. 225, pl. xiii. figs. 2 a-b; Alcock, Journ. Asiatic Soc. Bengal, lxvii. (2) p. 173 (1898).

One male specimen.

*Locality.* "Murray Island, reef."

*Distribution.* Red Sea to Tahiti.

#### CYMO MELANODACTYLUS, De Haan.

*Cymo melanodactylus*, Dana, U.S. Expl. Exp., Crust. i. p. 225, pl. xii. fig. 1; Alcock, Journ. Asiatic Soc. Bengal, lxvii. (2) p. 174 (1898).

A male specimen.

*Locality.* "Torres Straits."

*Distribution.* Ceylon to Fiji and Japan.

#### OZIUS GUTTATUS (Milne-Edwards).

*Ozius guttatus*, H. Milne-Edwards, Hist. Nat. Crust. i. p. 406; A. Milne-Edwards, N. Arch. Mus. Paris, ix. 1873, p. 239, pl. xi. fig. 1; Miers, Rep. Voy. 'Alert,' Crust. p. 228; De Man, Arch. Naturg. liii. (1) 1887, p. 291; Ortmann, Zool. Jahrb. Syst. vii. 1893, p. 476.

A female specimen, measuring 32 mm. in length by 48.5 mm. in breadth. The frontal teeth are considerably more prominent than in Milne-Edwards's figure.

*Locality.* "Torres Straits."

**PSEUDOZIUS DISPAR, Dana.**

*Pseudozius dispar*, Dana, U.S. Expl. Exp., Crust. i. p. 235, pl. xiii. fig. 9.

*Sphærozius dispar*, Stimpson, Proc. Acad. Philad. 1858 (1859), p. 85.

*Pilumnus nitidus*, A. Milne-Edwards, N. Arch. Mus. Paris, ix. p. 249, pl. x. fig. 2 (1873); De Man, Arch. Naturg. liii. (1) p. 305 (1887).

*Pseudozius dispar*, Ortmann, Zool. Jahrb. Syst. vii. p. 433 (1893).

Two specimens, the larger of which, an ovigerous female, differs somewhat from Milne-Edwards's figure as regards the outline of the carapace. The antero-lateral margin is considerably shorter than the postero-lateral. The greatest width is in the line of the penultimate antero-lateral teeth and well in front of the middle of the length. In the figure the greatest width is at about the middle at the level of the last pair of antero-lateral teeth. The description given by De Man applies accurately, in most points, to our specimen, except as regards the supposed sexual differences. He found the carapace narrower in a male specimen, the breadth-ratio being only 1.25 as against 1.37 in the female; and in the male the outer surface of the large hand was smooth with only a few granules near the proximal end, while in the female the whole surface was covered with granules as in the smaller chela. The latter difference between the sexes was also found by Ortmann. As regards the breadth of the carapace, our specimen is intermediate between the two examined by De Man, the ratio being 1.31. The measurements given by Milne-Edwards have evidently suffered from some misprint, but measurements taken from his figure of an adult male give a breadth-ratio of 1.41, considerably greater than that given by De Man for the female. As regards the granulation of the large cheliped, our specimen presents exactly the condition figured by Milne-Edwards and described by De Man as characterizing the male, the outer surface being smooth with a few granules grouped near the proximal end. Our second specimen, a minute and immature female, has more numerous granules on the large chela, which, however, is still much smoother than the small chela. In both cases the right cheliped is the larger.

De Man suggested the possible identity of Milne-Edwards's species with the *Pseudozius dispar* of Dana, and this suggestion has been accepted by Ortmann. Dana's figure is very similar to our specimens, and his description, though lacking in detail, applies perfectly, save in the one point that the finger of the large hand is said to be "smooth and round, and not channeled." In our specimens, as in De Man's account, the fingers of both hands are grooved. Dana gives the breadth-ratio of the carapace as 1.21, rather less than the narrowest individual examined by De Man. The table of generic characters given by Dana (*l. c.* p. 229) states that the carapace in this genus is "fere planus"; but that this does not apply to the species in question may be gathered from the fact that Stimpson refers it to his genus *Sphærozius*, which is defined as having the body subglobose. Stimpson, however, gives as a generic character "Margo frontalis et supra-orbitalis continuæ nec sinu nec incisura separatæ." In our specimens, as in De Man's description, the frontal lobes are separated from the supraorbital margin by a slight but

distinct notch. Ortmann retains the species in the original genus "weil die Antero-lateralzähne undeutlich sind."

*Locality.* "Murray Island, reef."

*Distribution.* Sulu Sea to New Caledonia.

#### PILUMNUS CURSOR, A. Milne-Edwards.

*Pilumnus cursor*, A. Milne-Edwards, N. Arch. Mus. ix. p. 244, pl. ix. fig. 4 (1873); Miers, Rep. Voy. 'Alert,' Crust. p. 223; De Man, Arch. Naturg. liii. (1) p. 299 (1887); Alcock, Journ. Asiatic Soc. Bengal, lxvii. (2) p. 195 (1898).

Three of our four specimens agree pretty closely with the descriptions of the authors cited above. They show some variation in the hairiness of the carapace: in two male specimens the body is covered with a scanty short pubescence, with which, near the front margin, a few longer hairs are intermixed; in a female individual, however, the long hairs are much more numerous and extend further back on the carapace. The hands are ornamented with rows of tubercles, not quite so thickly set as in Milne-Edwards's figure, interspersed with short hairs. The legs are a little longer than in the figure, and the merus of the first three pairs has a few spinules on its upper margin.

One specimen, a male infested by a Rhizocephalan parasite, differs in certain points from the others, but cannot, I think, be specifically separated from them. The outer surface of the larger (right) chela is here for the most part quite smooth, with only a few granules and hairs near the proximal end and along the upper margin, the groove on the dactylus is represented by a line of punctations, the sub-hepatic tubercle is wanting, and the ambulatory legs are even longer than in the more typical specimens. In the armature of the cheliped this specimen resembles *P. Andersoni*, De Man (Journ. Linn. Soc., Zool. xvii. p. 59, pl. iii. figs. 5, 6), from which, however, it is distinguished by the shape of the carapace, the antero-lateral margins being much shorter and the postero-lateral more nearly parallel than in that species.

*Localities.* "Murray Island, reef"; "Channel between reefs, Mer."

#### PILUMNUS PULCHER, Miers.

*Pilumnus pulcher*, Miers, Rep. Voy. 'Alert,' Crust. p. 219, pl. xxii. fig. A.

*Actumnus pulcher*, Ortmann, Semon's Forsch. Reise Austr., Crust. p. 52 (1894).

The larger of our two specimens is only 6 mm. long, but it agrees pretty closely with Miers's description and figure and with the much larger type specimens with which I have compared it. The chief difference is the somewhat greater length of the legs; in Miers's specimens the penultimate leg is about as long as the greatest breadth of the carapace, while in our larger specimen the carapace measures 6.5 mm. in breadth, and the corresponding leg nearly 8 mm. in length. Ortmann has referred this species to *Actumnus*, but the characters which he adduces hardly seem to justify its removal to that genus.

*Locality.* "Murray Island."

**PILUMNUS SEMINUDUS, Miers.**

*Pilumnus seminudus*, Miers, Rep. Voy. 'Alert,' Crust. p. 222, pl. xxi. fig. C.

Two female specimens, measuring about 6.25 mm. in length. Though little more than half the size of Miers's type specimen they agree very closely with it. In one individual the antero-lateral teeth are much less prominent than in the type, and the middle tooth of the right side is wanting. In both specimens the pubescence on the front part of the carapace is less developed, and there are a few longer hairs in a transverse row in front of the protogastric region. The species bears a considerable resemblance to the *Pseudozius dispar* referred to above, and perhaps the two should not be generically separated.

*Locality.* "Mabuiag."

**PILUMNUS LANATUS (Latr. ?), Miers.**

*Pilumnus lanatus* (Latr.), Miers, Rep. Voy. 'Alert,' Crust. p. 220, pl. xxi. fig. A.

A number of small and probably immature specimens are all but identical with the 'Alert' specimens described under this name by Mr. Miers. The close pubescence covering the body and limbs ends abruptly on the outer surface of the larger chela along a diagonal line drawn from the base of the dactylus above to the proximal angle below, the rest of the surface being smooth and polished. The antero-lateral teeth are smaller than in Miers's figure, the last tooth in particular being much reduced. A small, but distinct, sub-hepatic tubercle is present, the upper surface of the carapace is slightly uneven in front, and there is a well-marked tubercle on the hepatic region above. The chelæ are rather shorter, the lower finger is not hooked at the tip as in Miers's figure, and I cannot detect the spinules which he describes on the carpus of the ambulatory legs.

*Locality.* "Torres Straits."

**PILUMNUS LONGICORNIS, Hilgd.**

*Pilumnus longicornis*, Hilgendorf, Monatsb. Akad. Berlin, 1878, p. 794, pl. i. figs. 8, 9; var., Miers, Rep. 'Challenger' Brachyura, p. 157; Alcock, Journ. Asiatic Soc. Bengal, lxvii. (2) p. 193 (1898).

A male specimen is referred with some doubt to this species. The carapace measures 17 mm. in length and 23 mm. in breadth (exactly the dimensions of Hilgendorf's specimen), is strongly arched in the front part in an antero-posterior direction and slightly so from side to side. The three antero-lateral teeth are very prominent and conical, the second and third with spiniform points curved forwards. The acute sub-hepatic tubercle, though small, is visible from above, causing the antero-lateral margin to appear four-toothed. The external orbital angle is produced into a small triangular tooth. The postero-lateral margin is longer than the antero-lateral, and is slightly concave owing to the prominence of the last pair of antero-lateral teeth. The whole surface of the carapace bears scattered and rather coarse granules, only some of the broad, shallow, inter-regional grooves being smooth. The setæ covering the carapace are rather thick-set and moderately long, springing in pencils of four or five, of which one



is generally much longer than the rest. The front is much deflexed, the inner lobes broadly rounded, the outer small and spiniform. The upper orbital margin has two hardly visible fissures, and is, like the lower margin, only faintly granulated. The internal angle of the lower margin is acutely rounded. The sub-hepatic region bears a few granules near the outer margin besides the sub-hepatic tooth. The merus of the chelipeds has a stout blunt tooth near the distal end of its upper margin. The carpus has a number of granules on its outer surface, which is clothed with long setæ, and there is a sharp tooth at its inner angle. In the hand of the larger cheliped the greatest breadth is about equal to the length of the palm measured in the middle line, and the dactylus is about three-fourths of this length. The whole outer surface of the palm bears longitudinal rows of acute granules, with one or two smaller granules scattered in the rather wide interspaces between the rows. On the upper margin some of the granules become spiniform, and the whole surface bears numerous rather long setæ, which extend with the granulation on to the bases of both fingers. The fingers are slightly furrowed. The merus of the ambulatory legs has the upper edge terminating distally in a spine, behind which there is a notch running down on both faces of the joint as a short groove.

From Hilgendorf's account our specimen differs in the rather more concave postero-lateral margins; in the more prominent sub-hepatic tooth ("nur angedeutet"); in the much less distinct granulation of the orbital margins; and in having the whole outer surface of the hand covered with granules and setæ. The granules on the surface of the carapace also appear to be more numerous. Unfortunately both antennal flagella are wanting in our specimen. The regions of the carapace are not so distinctly marked as in Hilgendorf's figure, but they appear to be similarly disposed. The tooth on the distal end of the merus of the ambulatory legs is not indicated by Hilgendorf.

The 'Challenger' specimen described by Miers, and regarded by him as a variety of this species, differs from the type and agrees with our specimen in the characters of the orbital margin, of the larger cheliped, and of the ambulatory legs. The sub-hepatic tooth, however, is said to be deficient and the chelipeds are nearly equal in size.

*P. Sluiteri* of De Man (Weber, Reise Niederl. O.-Ind. ii. p. 283, pl. i. fig. 2, and (as *P. Forskalii*, M.-E.), Arch. Naturg. liii. (1) p. 295, pl. xii. fig. 1) is a closely allied species, but differs in the less prominent antero-lateral teeth and more granulated carapace, and in the absence of the notch and tooth on the merus of the ambulatory legs. *P. scabriusculus*, Ad. & Wh. (Zool. Voy. 'Samarang,' Crust. p. 44, pl. ix. fig. 5) has the antero-lateral teeth less prominent, wide, and denticulated.

*Locality.* "Fringing reef, Mer, Murray Island."

*Distribution.* E. Africa (Inhambane, Hilgendorf), to Tongatabu (Miers).

*PILUMNUS CRISTIPES*, n. sp. (Plate 1. figs. 1-3.)

Carapace closely covered with a short fur, which does not conceal the rather prominent regional areolæ. On removing the fur, a few scattered granules are seen, each bearing a tuft of short hairs. The front part of the carapace is strongly convex in an antero-

posterior direction, while the posterior part is flat. From side to side, in the line of the lateral teeth, the surface is only slightly convex. The strongly deflexed front is divided by a rather deep incision into two rounded lobes, and the outer angles form sharp downwardly directed teeth, not visible from above, separated by a groove from the supra-orbital angle. The upper margin of the orbit is interrupted by two short open fissures, and a third is present on the lower margin just below the external angle. The external angle of the orbit is not very prominent, rounded, and produced backwards for a short distance as a slight ridge above the level of the first antero-lateral tooth. The antero-lateral margin is equal in length to the postero-lateral, and is cut into four thick, bluntly rounded teeth, increasing in length from before backwards, covered with fur interspersed with granules.

The flagellum of the antenna is nearly one fourth the length of the carapace.

The ridges of the palate are distinct but not very prominent, and become obsolete before reaching the front margin of the buccal frame.

The chelipeds are very unequal; the merus is short, trigonous, the upper margin carrying a large rounded tooth separated by a narrow incision from the projecting rounded distal angle; the carpus has on its convex outer face scattered granules, partly arranged in oblique lines and interspersed with fur, and a transverse groove runs parallel to the distal margin; the hand of the larger cheliped (the right) has the palm but little longer than broad, with longitudinal rows of granules nearly hidden by the fur on its outer face; the fingers are stout, about one-half the length of the palm, with blunt rounded teeth on the inner edges; the dactylus has a patch of granules and hairs at its base, and both fingers are slightly grooved. In the smaller hand the granules on the outer face are less regularly arranged in rows.

The ambulatory legs have the merus with a sharp crest on its upper edge, rising gradually with a straight edge towards the distal end, where a narrow notch separates it from the prominent rounded distal tooth. In the first three pairs the anterior and posterior faces of the merus are smooth and nearly free from hair. In the last pair of legs the posterior face of the merus is closely furred. The carpus and propodus of all the legs are considerably expanded and flattened, covered with fur rather longer than that on the carapace, and the carpus has a deep longitudinal groove on the anterior and posterior faces. The dactylus of all the legs is stout and nearly cylindrical. The abdomen (female) has all seven joints free.

The form described above differs from all the species of *Pilumnus* known to me in the crested merus of the ambulatory legs, the feebly developed endostomial ridges, and the blunt teeth of the antero-lateral margin. In the first two of these characters it approaches the *P. dilatipes* of Adams & White (Zool. Voy. 'Samarang,' Crust. p. 44, pl. ix. fig. 4), for which Miers has proposed to constitute a separate genus *Lophopilumnus* (Rep. Chall. Brachyura, p. 148); but in that species the antero-lateral teeth are broad and denticulated and the meral crests are of very different shape and are not divided by a notch near the distal end. In the great convexity of the anterior portion of the carapace the species has some resemblance to an *Actumnus*, in which genus, however, the carapace is not

flattened posteriorly and is usually strongly arched from side to side. Dr. De Man has suggested to me a possible relationship with the genus *Lophoxanthus*. In that genus, however, the carapace is usually depressed and glabrous, and though Miss Rathbun has recently described a species *L. frontalis* (Proc. U.S. Nat. Mus. xvi. 1893, p. 236) forming an exception in both these respects, it does not appear to draw appreciably nearer to the present form. The whole aspect of our species, the shape of the front, and many other small points are so suggestive of *Pilumnus* that it seems best, for the present at any rate, to include it in that genus, though it certainly diverges considerably from the more typical species.

Length of carapace .....	20 mm.	Length of chela .....	18 mm.
Breadth        „ .....	28 „	„    dactylus .....	8 „
Length of larger cheliped .....	31 „	„    last leg .....	30 „

*Locality.* “Fringing reef, Mabuiag.”

#### ACTUMNUS SETIFER (De Haan).

*Pilumnus setifer*, De Haan, Faun. Japon., Crust. p. 50, pl. iii. fig. 3.

*Actumnus setifer*, A. Milne-Edwards, N. Arch. Mus. Paris, i. p. 287, pl. xv. figs. 5-5 b (1865); Alcock, Journ. Asiatic Soc. Bengal, lxvii. (2) p. 202 (1898).

Our four specimens show considerable variation in several points, but must all, I think, be referred to this common and widely distributed species. The smallest specimen is a female, and, although only 6.25 mm. in length, carries eggs. In this individual the lobulation of the carapace is not very pronounced, and the antero-lateral teeth are prominent and tipped with spiniform tubercles. In some of the larger specimens the lobules of the carapace are more prominent, the carapace is more convex, and the antero-lateral teeth are reduced to low, rounded lobes, on which the minute spiniform points are completely hidden by the dense pubescence covering the whole carapace. These differences, as well as slight variations in the relative breadth of the carapace, appear to be independent of age or sex. In a very large male, 17.5 mm. in length, from Sagami Bay, Japan, in the Museum of University College, the antero-lateral spines are very distinct, and the lobulation of the carapace is less pronounced than in a specimen only 7 mm. long in Prof. Haddon's collection.

*Localities.* “Flinders Entrance, near Mer, 20-30 fath.”; “S. of Orman's reef, 5-7 fath.”

#### TRAPEZIA FERRUGINEA, var. AREOLATA (Dana).

*Trapezia ferruginea areolata*, Ortmann, Zool. Jahrb. Syst. x. p. 206 (with synonymy); Alcock, Journ. Asiatic Soc. Bengal, lxvii. (2) p. 221 (1898).

One specimen, an ovigerous female about 10 mm. in length, having the lateral teeth of the carapace acute. De Man has pointed out (Arch. Naturg. liii. (1) p. 317) that this juvenile character is occasionally retained in adult individuals, though as a rule these teeth become obtuse (var. *inermis*, A. M.-E., N. Arch. Mus. Paris, ix. p. 259, pl. x. fig. 6).

The reticulations on the carapace of our specimen are rather larger and more symmetrically disposed than in Milne-Edwards's figure.

*Locality.* "Murray Island."

*Distribution.* Ceylon to Tahiti.

**TRAPEZIA CYMODOCE (Herbst).**

*Trapezia cymodoce*, Ortmann, Zool. Jahrb. Syst. x. p. 203 (with synonymy); Alcock, Journ. Asiatic Soc. Bengal, lxvii. (2) p. 219 (1898).

Three specimens are referable to this species as defined by Ortmann. The pubescence on the outer surface of the chela is rather scanty and not conspicuous in dried specimens, and the lower margin of the chela is faintly granular. The carpus of the chelipeds bears internally an acute spiniform tooth; only in one detached cheliped is this tooth blunt (*cf.* De Man, Arch. Naturg. liii. (1) p. 316).

*Locality.* "Murray Island, channels between reefs, 15-20 fath."

**TETRALIA GLABERRIMA (Herbst).**

*Tetralia glaberrima*, Ortmann, Zool. Jahrb. Syst. x. p. 209 (with synonymy); Alcock, Journ. Asiatic Soc. Bengal, lxvii. (2) p. 223 (1898).

Two specimens, one of which resembles the form named *T. nigrifrons* by Dana (U.S. Expl. Exp., Crust. i. p. 262, pl. xvi. fig. 2). The dark marginal band extends across the whole front edge of the carapace and halfway down the sides.

*Locality.* "Reef, Wyer."

*Distribution.* Red Sea to Marquesas.

**LISSOCARCINUS ORBICULARIS, Dana.**

*Lissocarcinus orbicularis*, Dana, U.S. Expl. Exp., Crust. i. p. 288, pl. xviii. figs. 1 a-e; A. Milne-Edwards, Arch. Mus. Paris, x. p. 418 (1861); Alcock, Journ. Asiatic Soc. Bengal, lxviii. (2) p. 20 (1899).

Six specimens presenting all the characters of Dana's species, but showing some slight variation in the distinctness of the antero-lateral teeth and in the concavity of the postero-lateral borders and consequent prominence of the lateral angles.

*Locality.* "Murray Island, reef."

*Distribution.* Mauritius to Fiji.

**CAPHYRA ROTUNDIFRONS, A. Milne-Edwards.**

*Camptonyx rotundifrons*, A. Milne-Edwards, N. Arch. Mus. Paris, v. 1869, p. 156, pl. vii. figs. 11-12.

*Caphyra rotundifrons*, A. Milne-Edwards, N. Arch. Mus. Paris, ix. 1873, p. 174.

Two female specimens of this very rare species are in the collection. They agree very exactly with Milne-Edwards's description and figure, the only observable differences being that the frontal lobes are slightly more prominent in the middle and are separated from the supra-orbital margin on either side by a shallow notch; the anterior margin of the merus of the chelipeds bears three teeth, and the merus of the second legs has no

spine on its upper border. The carapace of our larger specimen measures 12.25 mm. in length by 15.5 mm. in breadth.

*Locality.* "Torres Straits."

*Distribution.* New Caledonia and Samoa (*Milne-Edwards*).

**NEPTUNUS SANGUINOLENTUS (Herbst).**

*Lupa sanguinolenta*, Milne-Edwards, Hist. Nat. Crust. i. p. 451, & in Règne Anim., Crust. pl. x. fig. 1.

*Neptunus sanguinolentus*, A. Milne-Edwards, Arch. Mus. Paris, x. p. 319 (1861); Alcock, Journ.

Asiatic Soc. Bengal, lxviii. (2) p. 32 (1899).

Two small and imperfect specimens, the larger only 15 mm. in length, belong apparently to this common species, though the characteristic "ocelli" are very faintly indicated on the carapace.

*Locality.* "Torres Straits."

**NEPTUNUS PELAGICUS (L.).**

*Lupa pelagica*, Milne-Edwards, Hist. Nat. Crust. i. p. 450.

*Neptunus pelagicus*, De Haan, Faun. Jap., Crust. p. 37, pls. ix., x.; A. Milne-Edwards, Arch. Mus.

Paris, x. p. 320 (1861); Alcock, Journ. Asiatic Soc. Bengal, lxviii. (2) p. 34 (1899).

Two specimens, about 22 mm. in length, are no doubt referable to this common species, though they differ in some slight details from large specimens. In general shape and in the character of the antero-lateral teeth they approach the *N. armatus* of A. Milne-Edwards (*l. c.* p. 322, pl. xxxiii. fig. 2), but the external frontal teeth are not in our specimens obtuse, and the spine on the median supra-orbital lobe is indicated, though not so large as in full-grown specimens of *N. pelagicus*. As Ortmann has pointed out (Zool. Jahrb. Syst. viii. p. 75), it is very doubtful whether *N. armatus* is a distinct species. Milne-Edwards says of it: "Cette espèce est de tous les *Neptunus* connus la plus élargie"; while Miers, referring to the very specimen described by Milne-Edwards, states that "the carapace is relatively somewhat narrower . . . than in *N. pelagicus* of about the same size" (Rep. Voy. 'Alert,' Crust. p. 229).

*Locality.* "Fringing reef, Mabuiag."

**NEPTUNUS (ACHELOUS) GRANULATUS (Milne-Edwards).**

*Lupa granulata*, Milne-Edwards, Hist. Nat. Crust. i. p. 454.

*Amphitrite gladiator*, De Haan, Faun. Jap., Crust. p. 65, pl. xviii. fig. 1 (*not* pl. i. fig. 5).

*Achelous granulatus*, A. Milne-Edwards, Arch. Mus. Paris, x. p. 344 (1861).

*Neptunus (Achelous) granulatus*, Alcock, Journ. Asiatic Soc. Bengal, lxviii. (2) p. 45 (1899).

A female specimen, 12 mm. long, agrees well with De Haan's figure, except that, as in all young specimens, the lateral spines are more elongated.

*Locality.* "Murray Island."

**NEPTUNUS (ACHELOUS) GRANULATUS, var. UNISPINOSUS, Miers.**

*Achelous granulatus*, var. *unispinosus*, Miers, Rep. Voy. 'Alert,' Crust. p. 230, pl. xxiii. fig. B.

*Neptunus (Achelous) unispinosus*, Miers, Rep. Voy. 'Challenger,' Brachyura, p. 180; De Man, Zool.

Jahrb. Syst. viii. p. 558.



Two males, 7.5 and 11 mm. long respectively, agree with Miers's type specimen in the shape of the frontal lobes and in having only one spine on the posterior edge of the arm. The antero-lateral teeth, however, are not distinctly more spiniform, nor is the last tooth longer than in specimens of *A. granulatus* of similar size. The second spine of the posterior edge of the arm is represented by a slight rudiment, as it is, indeed, in the type specimen. I do not think that the form can be ranked as more than a variety of *A. granulatus*, as it was originally regarded by Miers.

*Localities.* "Sabai Channel"; "Murray Island."

#### THALAMITA PRYMNA (Herbst).

The forms of *Thalamita* in which the front is divided into eight lobes were distributed by A. Milne-Edwards among seven species and reunited by Kossmann into one, while more recent writers have expressed various views intermediate between these two extremes. Alcock has recently affirmed his belief in the correctness of Kossmann's view, while retaining, for the sake of convenience, separate specific names for some of the forms. Ten specimens collected by Prof. Haddon belong to this section of the genus and fall into three groups, not one of which agrees in all points with any of the described species:—

(a) A large male, the carapace of which measures 37 mm. in length by 59 mm. in breadth, agrees best on the whole with the descriptions of the typical *Th. prymna*, but presents certain points of difference. Comparing the frontal lobes with the figure given by De Man (Journ. Linn. Soc., Zool. xxii. pl. iv. fig. 5), the outer or fourth pair are much more strongly arcuate and resemble the figure of *Th. spinimana* (*l. c.* fig. 7); the third pair of frontal lobes are separated by an open fissure from the second or submedian, as in Dana's figure of *Th. crassimana* (U.S. Expl. Exp., Crust. pl. xvii. fig. 9 a); the submedian are slightly less prominent than the median lobes, which they distinctly overlap above, an arrangement which, according to A. Milne-Edwards (Arch. Mus. Paris, x. p. 362), "ne se voit jamais chez le *Th. prymna*." De Man's description and figure of *Th. cæruleipes* (Zool. Jahrb. Syst. viii. p. 568, pl. xiv. fig. 12 a) fits this specimen well as regards the third and fourth frontal lobes, but the median pair are stated to be wider than the submedian, while in the present instance the reverse is the case. The basal antennal joint carries a row of about four sharp spines besides some smaller granules. Milne-Edwards assigns to it only two or three spines, while Dana figures an irregularly toothed crest. The fourth antero-lateral tooth is very small, and the greatest breadth of the carapace is measured between the third pair of teeth. The cheliped differs from all descriptions of *Th. prymna* in having three spines instead of two on the upper margin of the hand, the additional spine being smaller than the other two and close to the proximal end.

(b) A male specimen, 21 mm. long by 33 mm. broad, has a row of granules on the basal antennal joint and a minute fourth antero-lateral tooth, and would therefore be referred by Milne-Edwards's table (*l. c.* p. 367) to *Th. Stimpsoni*, which De Man regards as a variety of *Th. Danae* (Journ. Linn. Soc., Zool. xxii. p. 78). With De Man's figure of *Th. Danae* (*l. c.* pl. iv. fig. 8) our specimen agrees in the nearly straight anterior edge

of the outer frontal lobes, but it differs in having the other three pairs of lobes separated only by slight notches. The abdomen does not present the peculiar outline figured by De Man (*l. c.* fig. 9), but he has since stated that this character is not constant (Notes Leyden Mus. xv. p. 285). In most other points this individual agrees closely with the above described specimen *a*, lacking, however, the third spine on the upper edge of the hand. A larger female specimen (31 mm. long) agrees with this, except that the fourth antero-lateral tooth is a little larger.

(c) Eight specimens, all of small size, including two ovigerous females of 8 mm. and 7 mm. in length respectively. The outer frontal lobes have a well-curved margin; the third lobes are narrow, rounded, and separated from the second by an open notch; the second or submedian lobes are very broad, about half as broad again as the median pair, which they distinctly overlap; the three inner pairs of lobes reach to about the same level. The fourth antero-lateral tooth is very minute or absent. The ridges of the hand have the same arrangement as in *Th. prymna*, but on the lower half of the outer face the ridges and the intervening spaces are quite smooth. The basal joint of the antenna is markedly shorter than in the other specimens described above.

These small specimens depart more widely from the typical *Th. prymna* than do the other specimens, but I have failed to identify them with any of the described species.

*Localities.* "Flinders Entrance, near Mer, 20-30 fath."; "Channels between reefs, Murray Island, 15-20 fath."

#### THALAMITA ADMETE (Herbst).

*Thalamita admete*, Milne-Edwards, Hist. Nat. Crust. i. p. 459; Dana, U.S. Expl. Exp., Crust. i. p. 281, pl. xvii. figs. 5 *a-c*; A. Milne-Edwards, Arch. Mus. Paris, x. 1861, p. 356.

*T. Savignyi*, A. Milne-Edwards, *l. c.* p. 357.

*T. admete*, Alcock, Journ. Asiatic Soc. Bengal, lxxviii. (2) p. 82 (1899).

Three female specimens, the largest 10.5 mm. long by 14.5 mm. broad, carrying ova. They appear to agree with the descriptions of *Th. Savignyi*, and are very similar to specimens so labelled in the British Museum. There appears, however, to be little doubt that this form is only a variety of *Th. admete*.

*Locality.* "Channel between reefs, Mer."

#### THALAMITA SIMA, Milne-Edwards.

*Thalamita sima*, Milne-Edwards, Hist. Nat. Crust. i. p. 460.

*Portunus (Thalamita) arcuatus*, De Haan, Faun. Jap., Crust. p. 43, pl. ii. fig. 2.

*Thalamita sima*, A. Milne-Edwards, Arch. Mus. Paris, x. p. 359 (1861); De Man, Zool. Jahrb. Syst. viii. p. 564 (1896); Alcock, Journ. Asiatic Soc. Bengal, lxxviii. (2) p. 81 (1899).

Six specimens, including an ovigerous female only 8.5 mm. in length, are referred to this species. In the larger specimens (20 mm. long) the antennal crest is smooth or nearly so, but in the smaller it is minutely granulated. In none are the margins of the median frontal lobes concave as described by De Man.

*Localities.* "Fringing reef and shore, Thursday Island"; "Channel between reefs, Murray Island."

**KRAUSSIA NITIDA**, Stimpson.

*Kraussia nitida*, Stimpson, Pr. Acad. Philad. 1858, p. 40; Miers, Rep. Voy. 'Alert,' Crust. p. 235; Henderson, Tr. Linn. Soc., (2) Zool. v. p. 379, pl. xxxvii. fig. 9 (1893); Alcock, Journ. Asiatic Soc. Bengal, lxviii. (2) p. 98 (1899).

A single male specimen appears to agree well with this species as briefly characterized by Stimpson and Miers and more fully by Henderson and Alcock. The frontal lobes are rather less deeply subdivided than in the figure given by Henderson. The whole surface of the carapace is covered with very minute granulations in short transverse rows. The outer surface of the hand is faintly granulated distally and near the upper edge.

*Locality*. "Channel between reefs, Murray Island."

**METOPOGRAPSUS MESSOR** (Forsk.).

*Metopograpsus messor*, Kingsley, Proc. Acad. Nat. Sci. Philad. 1880, p. 190; Ortmann, Zool. Jahrb. Syst. vii. 1894, p. 701.

A small specimen (8.5 mm. long) appears to belong to this widely distributed species. In the relative length of the propodus of the ambulatory legs it approaches the variety *gracilipes* of De Man (Notes Leyden Mus. xiii. p. 49), but the specimen is too immature for precise determination.

*Locality*. "Cockburn group (N. Queensland), shore."

**VARUNA LITTERATA** (Fabr.).

*Varuna litterata*, Kingsley, Proc. Acad. Nat. Sci. Philad. 1880, p. 205; Ortmann, Zool. Jahrb. Syst. vii. 1894, p. 713; De Man, Zool. Jahrb. Syst. ix. 1897, p. 112.

One female specimen.

*Locality*. "Torres Straits."

**OCCYPODA CERATOPHTHALMA** (Pallas).

*Ocypoda ceratophthalma*, Ortmann, Zool. Jahrb. Syst. x. 1897, p. 364 (with synonymy).

Five full-grown males and one female and a number of immature individuals are in the collection.

*Localities*. "Reef, Murray Island"; "Mer"; "Mabuiag."

**UCA TETRAGONON** (Herbst).

*Gelasimus tetragonon*, Kingsley, Proc. Acad. Nat. Sci. Philad. 1880, p. 143, pl. ix. fig. 11 (with synonymy); De Man, Notes Leyden Mus. xiii. 1891, p. 24, pl. ii. fig. 6; Ortmann, Zool. Jahrb. Syst. vii. 1894, p. 754.

*Uca tetragona*, Ortmann, Zool. Jahrb. Syst. x. 1897, p. 348.

A male specimen, in which the carapace measures 13 mm. in length, is referred to this species. In the armature of the fingers the large chela agrees precisely with Kingsley's figure (*l. c.*), but the fingers themselves are much shorter, not equalling the palm in length, and the outline of the chela therefore resembles the figure of *G. variatus* which Kingsley (*l. c.* pl. x. fig. 32) copies from Hess. The last-named species is regarded by

De Man and Ortmann as synonymous with the present. De Man's description and figure (*l. c.*) agree closely with our specimen, save that the orbits are more oblique and the fingers of the chela much longer in the figure.

*Locality.* "Torres Straits."

*Distribution.* Red Sea to Sandwich Islands.

CERATOPLEX (?) sp.

An imperfect dried specimen resembles rather closely in general shape the *Ceratoplex ciliata* of Stimpson, as figured by Miers (Chall. Rep., Brachyura, p. 234, pl. xix. fig. 3). It differs, however, in the broader meral and carpal joints of the walking-legs (Miers states that in his specimen the legs "are rather more slender than in the description of Dr. Stimpson") and in the rather stouter fingers of the chelipeds. It differs, moreover, not only from Miers's figure, but also from the generic diagnosis in the fact that the antero-external angle of the merus of the third maxillipeds is rounded off and not distinctly produced.

*Locality.* "Torres Straits."

CALAPPA HEPATICA (L.).

*Calappa hepatica* (L.), Alcock, Journ. Asiatic Soc. Bengal, lxx. (2) p. 142 (1896).

Three female specimens, the carapace of the largest measuring 40 mm. in length by 60 mm. in breadth.

*Locality.* "Murray Island."

CRYPTOCNEMUS HADDONI, n. sp. (Plate 1. figs. 4-8.)

*Description.* The margins of the lateral wings of the carapace are convex, presenting no salient lateral angle such as is present in *C. pentagonus*, Stps., and passing, with scarcely an indication of a postero-lateral angle, into the posterior margin, where the curve meets its fellow in the middle line in a slight re-entrant angle. The lateral margin is continued on to the dorsal surface of the carapace behind the hepatic region on either side as a faintly marked ridge which soon dies out. The front is obtusely triangular and slightly reflexed, the straight line of each side being continued beyond the orbit to the prominent hepatic angle. On the flat dorsal surface a low longitudinal keel runs from the tip of the rostrum to near the posterior edge of the carapace, being most prominent on the cardiac region, and the branchial regions are very slightly inflated. The surface of the carapace is perfectly smooth; the posterior and lateral margins, as well as the faint ridges on the hepatic regions, are microscopically beaded. The antennular fossæ are transverse. The third maxillipeds have the merus equal in length to the ischium, acutely triangular and projecting well beyond the margin of the buccal area, though not so far as to be visible from above. The exopod is equal in breadth to the ischium; its outer edge is convex, the tip truncate and very slightly concave. The chelipeds have the merus trigonous, with two minutely granular lines on its lower margin; the carpus has a slight keel exteriorly; the hand is compressed, the edges acute, the palm being one and a half times

as long as broad; the fingers are grooved and one-third the length of the palm. The walking-legs have the merus compressed and crested above and below, the carpus and propodus with a double keel on the upper edge and the dactylus styliform. The abdomen of the female is very nearly circular in outline, and the first, second, and last somites are free. The whole of the under surface is quite smooth.

Length 5.5 mm.; breadth 7.25 mm.

Of the four described species of *Cryptocnemus* our new form approaches most closely to the type, *C. pentagonus* of Stimpson (Pr. Acad. Philad. 1858, p. 161), figured by Miers (Proc. Zool. Soc. 1879, p. 43, pl. ii. fig. 5), whose imperfect specimen I have examined. In that species, however, the wings of the carapace are produced into acute lateral angles, and the straight postero-lateral and posterior margins meet at an obtuse angle; the front is more strongly reflexed and more acute, the branchial regions are more convex, the lateral margins are not continued on to the dorsal surface in front, and the granulation of the posterior and lateral margins is more pronounced than in the present species; the antennular fossæ are oblique and the palp of the external maxillipeds is rounded, not distinctly truncate, at the tip. In *C. Holdsworthi*, Miers (Tr. Linn. Soc., (2) Zool. i. p. 241, pl. xxxviii. figs. 30-32, 1878), the lateral margins are at right angles to the posterior margin, and there are two oblique carinæ running from the cardiac region to the posterior corners on the dorsal surface of the carapace. *C. Grandidieri*, A. Milne-Edwards (Ann. Soc. Ent. France, (4) v. p. 135, pl. vi. fig. 4, 1865), resembles *C. Holdsworthi* in general shape, but has a broadly truncate front, the posterior border is notched in the middle, and the surface of the carapace has three granulated carinæ diverging from the centre to the rostrum and the two posterior corners respectively. Finally, *C. obolus*, Ortmann (Zool. Jahrb. Syst. vi. p. 576, pl. xxvi. fig. 12, 1892), has a nearly circular outline, the rostrum is bifid, and the hepatic prominences are acute, almost spiniform, teeth.

*Locality*. "Channel between reefs, Mer."

**OREOPHORUS FRONTALIS**, Miers.

*Oreophorus frontalis*, Miers, Rep. Voy. 'Alert,' p. 254, pl. xxvi. fig. B.

A comparison of our eight individuals with the unique type specimen leaves no doubt as to their identity. Miers's figure does not represent quite accurately the proportions of the carapace, the relative length, and especially the prominence of the whole frontal region, being considerably exaggerated.

*Localities*. "Flinders Entrance, near Mer"; "Channels between reefs, Murray Island."

**MYRA FUGAX** (Fabr.).

*Myra fugax* (Fabr.), Alcock, Journ. Asiatic Soc. Bengal, lxx. (2) p. 202 (1896) (and synonyms).

*M. pentacantha*?, Alcock, l. c. p. 204.

Two male specimens, of small size and therefore difficult to determine with certainty, are probably young forms of this common and variable species. The smaller of the two possesses five spines on the posterior margin of the carapace and a well-marked tubercle



on the intestinal region. It agrees closely with the type specimens of *M. dubia*, Miers (Proc. Zool. Soc. 1879, p. 42), from Japan, which Miers subsequently (Rep. 'Challenger' Brachyura, p. 314) identified with the *M. coalita* of Hilgendorf (Monatsber. Akad. Berlin, 1878, p. 812, pl. i. figs. 6, 7), ranking it as a variety of *M. fugax*. The *M. pentacantha* of Alcock, of which I have examined specimens, differs chiefly in the pubescence of the frontal region. This provisional species is regarded by its author as being probably the young form of *M. fugax*.

*Locality.* "Channels between reefs, Murray Island."

**MYRA AUSTRALIS, Haswell (?).**

*Myra australis*, Haswell, Proc. Linn. Soc. N. S. Wales, iv. p. 50, pl. v. fig. 3 (1879); Haswell, Cat. Austr. Crust. p. 122; Miers, Rep. 'Challenger' Brachyura, p. 315.

A female specimen, 20 mm. in length, is provisionally referred to this species on account of its general resemblance to specimens so named in the collections of the British Museum. From these and from Haswell's account, however, it differs in the shorter neck-region, in the finer and closer granulation of the surface, and in the absence of any distinct group of granules on the intestinal region.

*Locality.* "Channel between reefs, Mer."

**LEUCOSIA LONGIFRONS, var. PULCHERRIMA, Miers.**

*Leucosia pulcherrima*, Miers, Tr. Linn. Soc., (2) Zool. i. p. 236, pl. xxxviii. figs. 4-6 (1877); Haswell, Proc. Linn. Soc. N. S. Wales, iv. p. 46 (1879).

*L. splendida*, Haswell, l. c. p. 47, pl. v. fig. 1.

*L. longifrons*, var. *pulcherrima*, Alcock, Journ. Asiatic Soc. Bengal, lxx. (2) p. 219 (1896).

A male specimen, agreeing minutely with Miers's type specimen, save that the "thoracic sinus" is rather more contracted. Apart from the colour-markings, Alcock states that this variety is distinguished from the typical *L. longifrons* by having the surface of the carapace slightly punctate instead of perfectly smooth, and by the stronger dorsal and ventral keels on the propodites of the ambulatory legs. Neither of these characters is so well marked in the Torres Straits specimen as in some specimens from Yokohama which I refer to *L. longifrons*. The carapace of the present specimen is much distorted, being swollen on one side, probably by the presence of an epicarid parasite in the branchial chamber.

*Locality.* "Channel between reefs, Murray Island, 15-20 fath."

**LEUCOSIA HASWELLI, Miers.**

*Leucosia Haswelli*, Miers, Rep. 'Challenger' Brachyura, p. 324, pl. xxvii. fig. 2; Alcock, Journ. Asiatic Soc. Bengal, lxx. (2) p. 222 (1896).

Our specimen shows an almost precise agreement with the descriptions of Miers and Alcock and with the type specimens in the British Museum. The inner (or lower) margin of the hand is defined by two distinct rows of fine granules, the lower replacing the row of punctations of Alcock's description.

*Locality.* "Fringing reef and shore, Thursday Island."

**PSEUDOPHILYRA TRIDENTATA, Miers.**

*Pseudophilyra tridentata*, Miers, Proc. Zool. Soc. 1879, p. 41, pl. ii. fig. 4; Alcock, Journ. Asiatic Soc. Bengal, lxx. (2) p. 250 (1896).

Our specimen, a male, agrees closely with Miers's type specimen, which, though described as a male, is apparently a sterile female. The inferior hepatic prominences are in our specimen placed a little further forward, so that they are visible from above in front of the superior prominences. The figure which accompanies Miers's description is a very indifferent representation of the type specimen, the whole frontal region, for instance, appearing relatively much too broad. The following are the approximate dimensions of the type and of our specimen:—

	Type specimen.	Torres Straits specimen.
Length of carapace .....	10 mm.	13·5 mm.
Breadth „ .....	8·5 „	11·5 „
Height „ .....	5·5 „	7·0 „
Width of front between external orbital teeth ...	2·35 „	2·75 „
Length of cheliped .....	.....	21·0 „
„ palm .....	.....	7·0 „
Width of palm .....	.....	3·5 „
Length of fingers .....	.....	3·0 „

Alcock's description applies very well to the specimen before me, except that he states the hand to be about "half as long again as broad." As will be seen from the figures given above, the palm alone, exclusive of the fingers, is twice as long as broad. Each finger carries a low obtuse tooth on the inner edge about the middle of its length.

*Locality.* "Torres Straits."

*Distribution.* Persian Gulf (*Alcock*); S. Japan (*Miers*).

**ARCANIA GRACILIPES, Bell (?).**

*Arcania gracilipes*, Bell, Trans. Linn. Soc. xxi. p. 310, pl. xxxiv. fig. 9 (1855); Alcock, Journ. Asiatic Soc. Bengal, lxx. (2) p. 270 (1896).

A male specimen, the carapace of which measures about 7 mm. in length and in breadth, with chelipeds about 15 mm. long, is referred with some doubt to this species. Compared with Bell's type specimen, it differs in the greater excavation of the hepatic regions above and the consequent greater prominence of the neck-region. The front (between the orbits) is also more prominent at the outer corners, so that the orbits have a more lateral position. The carapace, as a whole, appears much less inflated, and the inter-regional grooves, especially the branchio-cardiac grooves, are deeper. The marginal tubercles are less prominent, and the whole surface is covered with closely-set depressed and smooth granules. In the type the granules are more widely spaced and more or less distinctly capitate or fungiform. Some phrases of Alcock's description, the "sunken" hepatic region and the carapace "closely covered with flat discoidal granules," are more suggestive of our specimen than of the type.

*Locality.* "Flinders Entrance, Mer, 20-30 fath."

Genus *PALICUS*, Philippi.

(= *Cymopolia*, Roux.)

The most diverse opinions have been expressed as to the systematic position of this genus, and although it retains its place among the Dorippidæ in Bouvier's recent revision of that family (Bull. Soc. Philomath. Paris, (8) ix. 1898), there appears to be considerable reason to doubt the correctness of this view. Without attempting to enter on a discussion of the question, I may note that the penial appendages of the male are (in the single specimen I have examined as to this point) distinctly exerted from the sternum at some distance from the bases of the last pair of legs. With regard to the disposition of these parts in the Dorippidæ, the statements of authors are conflicting. Miers, for instance, writes: "The sexual appendages in the male are exerted from the sternum" (Rep. 'Challenger' Brachyura, p. 326), while Ortmann has "männliche Genitalöffnung stets coxal gelegen" (Bronn, Thier-Reich, Crust. ii. p. 1157). I find that in *Dorippe* the latter statement is the more correct, although the penial tube lies, at its base, between two processes of the sternum, which may in (*D. sima*) meet above and form a complete ring. The greater separation of the place of emergence of the penes from the bases of the legs in *Palicus* tends to support the view of those authors who would ally this genus with the Catometopa.

The description and figures of *Pleurophricus spinipes* given by De Man (Arch. Naturg. liii. (1) p. 344, pl. xv. fig. 1, 1887) are strongly suggestive of close affinity between that genus and the present. The general outline of the carapace, the relative length of the four pairs of ambulatory legs, the shape of the third maxillipeds, and the very broad sternum are among the points of resemblance between the two. *Pleurophricus cristatipes*, A. M.-E., the type and only other species of the genus, appears, from Milne-Edwards's figure (Journ. Mus. Godeffroy, Heft iv. pl. xii. fig. 6), to have less resemblance to *Palicus*, the ambulatory legs being all of about the same length. De Man considers *Pleurophricus* to be more nearly allied to Corystoidea than to any other group of Brachyura. Milne-Edwards had placed it among the Oxystomata, while Miers suggests that its place is with the Schizophrysinae among the Oxyrhyncha (Journ. Linn. Soc., Zool. xiv. p. 660).

*PALICUS JUKESII* (White). (Plate 1. figs. 9-13.)

*Cymopolia Jukesii*, White, Jukes's Voy. 'Fly,' ii. App. p. 338, pl. ii. fig. 1 (1847); Miers, Zool. Voy.

'Erebus' and 'Terror,' vol. ii. no. xx. Crust. p. 3, pl. iii. figs. 4 a-c (1875) (1874?); Miers, Rep.

'Challenger' Brachyura, p. 335 (1886).

*C. carinipes*, Paulson, Crustacea of the Red Sea (Russian), Kiev, 1875, p. 73, pl. ix. figs. 4-4 a.

*Palicus Jukesii*, Bouvier, Bull. Soc. Philomath. Paris, (8) ix. p. 12 (sep. copy) (1898).

**Description of male.** The carapace is subquadrate in outline, with the lateral margins slightly convergent anteriorly. The surface is very uneven, being thrown into rounded transverse ridges, of which two, crossing the carapace at the level of the gastric and cardiac regions respectively, are the most conspicuous. The prominent regions are coarsely granulated and the whole surface is nearly free from hairs. The front is divided into two rounded lobes defined from the orbital margin on either side by a

distinct notch. The upper margin of the orbit presents two fissures, of which the inner is a V-shaped notch, while the outer is closed and inconspicuous. The external orbital tooth is blunt, and behind it on the lateral margin are two well-marked teeth, with a slight indication of a third. The two lobes of the lower orbital margin are sharply triangular, the inner being the more prominent, and have the edges hardly or not at all granulated. On the sub-hepatic region just behind the lower orbital margin there is a blunt transversely elongated tubercle or short ridge.

The eye-stalk carries about three tubercles, the largest of which, close to the corneal region on the anterior edge, is in the form of a flattened lobe with a rounded distal edge. The basal joint of the antenna has a very prominent longitudinal keel on its ventral surface, and externally a blunt laterally compressed lobe springs from near the base of the joint and is directed forwards and outwards. The two succeeding joints of the peduncle are narrow and cylindrical. The ischium of the third maxillipeds has two marked diagonal ridges on its ventral surface. The merus is produced distally external to the insertion of the carpus as a conspicuous rounded lobe extending to more than half the length of the carpus.

The chelipeds in the single male specimen examined are rather feeble and are perhaps not fully developed. The palm is subcylindrical and has faint longitudinal ridges on its outer surface.

The ambulatory legs of the second and third pairs have the upper (or anterior) edge of the merus cut into four teeth. The crest on the anterior margin of the carpus has no distinct proximal lobe, but the distal lobe is a sharp tooth set a little way back from the end of the joint. The propodus is much expanded, being three and a half times as long as broad, and the anterior edge is strongly convex. In the second pair of ambulatory legs (but in none of the others) there is, on the ventral surface of the merus at its proximal end, a short longitudinal ridge, which is minutely and regularly granulated. The abdomen of the male has all the somites free and each is crossed about the middle of its length by a transverse ridge. The lateral margins are slightly concave and form a distinct angle at the sixth somite. The sternum and abdomen are finely granulated. The first abdominal appendages of the male are stout and the two lobes of the tip are closely approximated, the outer extending a little beyond the inner.

The specimen from which my description and figures are taken agrees minutely with the specimens in the British Museum with which I have compared it. According to Miers's figure, the abdomen of the female is subcircular in outline, with all the somites distinct and transversely ridged as in the male.

*Cymopolia carinipes* of Paulson is very likely identical with the present species. His figures show the general shape of the carapace to be very similar, though the lateral margins are more nearly parallel. The transverse grooves and ridges of the surface and the granulation of the more prominent parts correspond with the specimen here described and figured. Paulson's figure of the entire animal (*l. c.* fig. 4) is, apparently, inaccurate as regards the shape of the frontal lobes, which his enlarged figure (fig. 4 *a*) shows to differ but slightly from the present form. The outer of the two fissures in the

supra-orbital margin is represented as open and V-shaped. The lower orbital margin, the tubercles on the eye-stalk, the basal joint of the antenna, and the external maxillipeds are all figured almost exactly as in our specimen. The first pair of walking-legs are rather stouter. The most marked difference, however, is that the tubercle on the under-side of the hepatic region is more strongly developed, being represented by a curved transverse ridge, from the outer end of which a row of granules (not found in our specimen) runs backwards for a short distance parallel to the lateral margin of the carapace.

*Locality.* "Torres Straits."

*Distribution.* Sir C. Hardy Island (Torres Straits) (*White*); Port Denison (*Haswell*); Celebes Sea (*Miers*); Red Sea (*Paulson*).

*PALICUS WHITEI* (Miers). (Plate 2. figs. 14-19.)

*Cymopolia Whitei*, Miers, Rep. Voy. 'Alert,' Crust. p. 551, pl. xlix. fig. C (1884).

*Palicus Whitei*, Bouvier, Bull. Soc. Philomath. Paris, (8) ix. p. 12 (sep. copy) (1898).

The lateral margins of the carapace are more nearly parallel than in *P. Jukesii*. The surface is less uneven, the transverse ridges being less marked, but the regions are fairly prominent and well-defined, though there is some variation in these respects among our specimens. The granulation of the surface is much finer and there is a scanty short pubescence interspersed among the granules. The frontal lobes are separated from the upper orbital margin on each side by a shallow concavity. Both the fissures of the upper orbital margin are open and V-shaped, while a third, present in some members of the genus, is slightly indicated by a notch at the base of the outer orbital tooth. This tooth is generally more acute than in *P. Jukesii*, but the two succeeding teeth on the lateral margin are less prominent than in that species. The lobes of the lower margin of the orbit are low and rounded, and the edge is finely granulated. There is no tubercle on the sub-hepatic region behind the orbital margin. The basal joint of the antenna bears a slight longitudinal ridge on its ventral face and is produced externally into a broad rounded lobe, flattened dorso-ventrally and projecting into the orbit. The two succeeding joints are robust, the third joint especially being expanded and compressed.

The large prominence on the eye-stalk has a peculiar and characteristic form. It is a crescentic or sickle-shaped blade, springing from a narrow base near the distal end of the anterior edge of the eye-stalk, and curving over, close to but free from the corneal surface, terminating externally in an acute point.

The ischium of the third maxillipeds is only faintly ridged on its ventral face, and the antero-external process of the merus is very small, not reaching to one-half the length of the carpus. The chelipeds are feeble in both sexes, the palm cylindrical, without ridges, but faintly granular and pubescent. The second and third pairs of walking-legs have the merus pubescent and faintly granulated, but without teeth on the margins. The anterior crest of the carpus has rounded proximal and distal elevations, the latter close to the end of the joint. The propodus is considerably narrower than in *P. Jukesii*,



being nearly four times as long as broad, and the anterior edge is only slightly convex. The granulated ridge on the underside of the merus of the second pair is present as in *P. Jukesii*.

The abdomen of both sexes is smooth, beset with small scattered setæ. The fourth, fifth, and sixth somites are fused together, but the sutures are faintly visible. In the male the sides of the abdomen are straight, convergent, and curve gently inwards from the base of the last somite to the tip without any distinct angle.

The first abdominal appendages of the male are slender, and the terminal lobes are divergent, the outer lobe being twice as long as the inner.

Our specimens differ from Miers's type specimens in the greater robustness of the second and third pairs of ambulatory legs, the merus and, to a less extent, the propodus being distinctly broader. In all other characters, however, the agreement is complete.

*Locality.* "Torres Straits."

*Distribution.* Seychelles, 4-12 fath. (*Miers*).

*PALICUS SERRIPES* (Alcock & Anderson). (Plate 2. figs. 20-22.)

*Cymopolia serripes*, Alcock & Anderson, Journ. Asiatic Soc. Bengal, lxiii. pt. 2 (1895) (? 1894), p. 208; Illustr. Zool. 'Investigator,' Crust. pl. xxiv. fig. 7 (1896).

*Palicus serripes*, Bouvier, Bull. Soc. Philomath. Paris, (8) ix. p. 12 (sep. copy) (1898).

Carapace with lateral margins convergent anteriorly, the surface leaving the regional areas well-defined but not very prominent, beset with rather coarse granulations on the more prominent parts. Posteriorly the granulations tend to become squamiform, and there is a line of conspicuous scale-like elevations just within the posterior and postero-lateral margins. Scattered hairs occur among the granules, more numerous on the depressed portions of the surface. The front is four-lobed; the inner lobes are acutely rounded and depressed, and extend beyond the outer lobes, which are low, rounded, slightly recurved, and hardly defined from the orbital margin. The upper margin of the orbit has two deep V-shaped fissures separated by an acute tooth, and a shallower notch at the base of the outer orbital tooth. The latter is acute, and is separated by a short interval from the first of the four subequal antero-lateral teeth. The lower margin of the orbit is convex in its outer part, concave internally, and terminates in a sharp internal orbital tooth. Just behind and parallel to the infra-orbital margin is a curved granulated ridge terminating internally in a small tubercle close to the tubercle which forms the anterior corner of the buccal frame. The basal joint of the antenna is produced externally into a flattened lobe, similar to, but smaller than, that found in *P. Whitei*, while the ventral face of the joint bears a row of three or four small tubercles in place of the longitudinal ridge found in that species. The two succeeding joints are rather elongated and cylindrical. The flagellum extends well beyond the outer angle of the orbit. The eye-stalk bears numerous, low, rounded tubercles, two of these on the anterior margin being larger than the others. The ischium of the third maxillipeds is nearly smooth on its ventral surface, and the merus has a well-developed antero-external

process with a small acute tooth at its tip. The exopod is broader than in the two preceding species. The cheliped of our single imperfect specimen is rather short and stout, the palm compressed, with rows of granules on its upper edge and outer face. The first pair of legs have the merus granulated and with a stout tooth at the distal extremity of its upper (or anterior) edge. The propodus and dactylus have each a few serrations on the lower edge. The merus of the second and third pairs is granulated, the granules becoming stout teeth on the upper and lower margins. The anterior crest of the carpus has two prominent teeth, with smaller serrations between. The propodus is about two and a half times as long as broad, the upper edge nearly straight, the lower edge serrate. The dactylus is broad and has three or four coarse and somewhat irregular teeth on its lower edge. There is no granulated ridge on the underside of the merus of the second pair.

The single, much injured, female specimen from which the above description is taken agrees well with the description of Alcock and Anderson. The figure which they give, however (taken from a larger specimen), differs in some details. The outer lobes of the front are much less prominent, so that the front appears two-lobed; the first lateral tooth follows close upon the extra-orbital and is separated by a slight interval from the second; the granulation of the carapace appears to be less coarse, and more restricted to the prominent lobules.

*Locality.* "Torres Straits."

*Distribution.* "Madras coast, shallow" (*Alcock & Anderson*).

#### **ACHÆUS AFFINIS, Miers.**

*Achæus affinis*, Miers, Rep. Voy. 'Alert,' Crust. p. 188; De Man, Arch. Naturg. liii. (1) p. 218 (1887); Alcock, Journ. Asiatic Soc. Bengal, lxiv. (2) p. 172 (1895).

A male specimen 5.5 mm. long is referred to this species. It is much smaller than any of the specimens of *A. affinis* with which I have compared it, but it agrees with them in the characteristic points of the tuberculated eye-stalks and the bilobed cardiac tubercle. As De Man points out, the eye-stalk carries a small tubercle near the tip in addition to the large one at the middle of its length, and a small tubercle also lies behind the bilobed eminence on the cardiac region. Our specimen has four granules on the gastric region, two median and two lateral. The free part of the antenna is only a little shorter than the carapace. The neck is rather longer than in the type specimen, and the carapace as a whole is a little narrower. As in Miers's account, the merus of the chelipeds is "somewhat trigonous," rather than "fast cylindrisch" as De Man describes it.

*Locality.* "Channel between reefs, Murray Island, 15-20 fath."

#### **PARATYMOLUS SEXSPINOSUS, Miers.**

*Paratymolus sexspinus*, Miers, Rep. Voy. 'Alert,' Crust. p. 261, pl. xxvii. fig. B; Henderson, Trans. Linn. Soc., (2) Zool. v. p. 352 (1893).

In our single perfect specimen, which I have compared with Miers's type, the rostrum

is hardly emarginate and the second antero-lateral tooth is less prominent than in Miers's figure.

This species is recorded from India (Tuticorin) by Prof. Henderson, though it is omitted (probably through inadvertence) from Alcock's revision of the Indian Oxyrhyncha.

*Localities.* "Channel between reefs, Mer"; "Mabuiag" (fragmentary specimen).

#### ONCINOPUS ARANEA, De Haan.

*Inachus (Oncinopus) aranea*, De Haan, Faun. Japon., Crust. p. 100, pl. xix. fig. 2.

*Oncinopus aranea*, Adams & White, Zool. Voy. 'Samarang,' Crust. p. 3.

*O. neptunus*, Adams & White, l. c. p. 1, pl. ii. fig. 1.

*O. aranea*, Alcock, Journ. Asiatic Soc. Bengal, lxiv. (2) p. 183 (1895).

Five female specimens, showing considerable variation in the relative prominence of the frontal lobes and in some other details. Alcock describes the antennæ as "extremely short, reaching only just beyond the tip of the rostrum": in our specimens, however, as in the figure of Adams & White, the flagella of the antennæ reach far beyond the tip of the rostrum.

*Locality.* "Channel between reefs, Mer."

#### XENOCARCINUS TUBERCULATUS, White.

*Xenocarcinus tuberculatus*, White, Proc. Zool. Soc. 1847, p. 119; A. Milne-Edwards, N. Arch. Mus.

Paris, viii. p. 253, pl. xii. figs. 1 a-g (1872); Alcock, Journ. Asiatic Soc. Bengal, lxiv. (2) p. 192 (1895); Alcock & Anderson, Illust. Zool. 'Investigator,' Crust. pl. xxxiii. figs. 3, 3a (1898).

A single, much damaged, male specimen, agreeing fairly well with Milne-Edwards's fig. 1, save that the carapace is much narrower.

*Locality.* "Murray Island."

#### HUENIA PROTEUS, De Haan.

*Maia (Huenia) proteus*, De Haan, Fauna Japon., Crust. p. 95, pl. xxiii. figs. 4-6.

*Huenia proteus*, Alcock, Journ. Asiatic Soc. Bengal, lxiv. (2) p. 195 (1895).

The series of this well-known species comprises two young males, an adult and a young female, and a "sterile" female in which only the 5th and 6th somites of the abdomen are fused.

*Localities.* "Channel between reefs, Mer"; "South of Orman's reef, 5-7 fath."

#### MENAETHIUS MONOCEROS, Latr.

*Menaethius monoceros*, Latr., Milne-Edwards, Hist. Nat. Crust. i. p. 339.

*M. angustus*, Dana, U.S. Expl. Exp., Crust. i. p. 120, pl. iv. figs. 5 a-b.

*M. monoceros*, Alcock, Journ. Asiatic Soc. Bengal, lxiv. (2) p. 197 (1895).

Two specimens of this very variable species approach most closely to the form named *M. angustus* by Dana, but the rostrum is rather shorter.

*Localities.* "Murray Island"; "Sabai Channel."

**HYASTENUS SPINOSUS, A. Milne-Edwards.**

*Hyastenus spinosus*, A. Milne-Edwards, N. Arch. Mus. Paris, viii. p. 250 (1872); Miers, Rep. 'Challenger' Brachyura, p. 56; Alcock, Journ. Asiatic Soc. Bengal, lxiv. (2) p. 211 (1895).

A female specimen, about 25 mm. in total length, agrees with the characters of this species as briefly indicated by Milne-Edwards and by Alcock, except that the lateral epibranchial spines appear rather small. It is identical with specimens in the British Museum referred to this species by Mr. Miers. An ovigerous female 20 mm. long differs in possessing a small acute granule on the cardiac region and three small tubercles (besides the epibranchial spine) on each branchial region. The two gastric spines are very small, but in other respects the specimen appears to agree with this species.

*Localities.* "Murray Island"; "South of Orman's reef, 5-7 fath."

**HYASTENUS ORYX, A. Milne-Edwards.**

*Hyastenus oryx*, A. Milne-Edwards, N. Arch. Mus. Paris, viii. p. 250, pl. xiv. fig. 1 (1872); De Man, Arch. Naturg. liii. p. 224, pl. vii. fig. 2 (1887); Alcock, Journ. Asiatic Soc. Bengal, lxiv. (2) p. 214 (1895).

Of the two specimens which I refer to this species, one, a female about 16 mm. in total length, agrees closely with the example figured by De Man, the rostral spines being rather less than one-fourth of the total length and strongly divergent. In a male specimen about 18 mm. long the rostral spines are more than one-third of the total length and quite parallel, and the whole carapace is rather narrower and not quite so much contracted in front, though still much more so than in Milne-Edwards's figure. The parallel rostral spines of the latter specimen give it a certain resemblance to *H. Sebae*, White (Seba, Thesaurus, iii. pl. xviii. fig. 12), in which, however, the distal parts of the much longer spines are divergent. In the specimens of *H. Sebae* which I have examined the carapace is much less tuberculated than in the present specimens. The chelipeds of our male specimen resemble Milne-Edwards's figure, but the hands are rather less expanded distally, and the serrated edges of the fingers meet for about half their length instead of only at the tip as Alcock states.

*Locality.* "South of Orman's Reef, 5-7 fath."

**HYASTENUS CONVEXUS, Miers.**

*Hyastenus convexus*, Miers, Rep. Voy. 'Alert,' Crust. p. 196, pl. xviii. fig. B; Henderson, Trans. Linn. Soc., (2) Zool. v. p. 344 (1893).

A male specimen of 10 mm. and a female of 13 mm. total length are referred with some doubt to Miers's species, with which they agree in the very convex gastric region and in the absence of spines from the carapace. They differ chiefly in the shorter rostral spines, which in the female are less than one-fourth of the total length. In the male there are minute acute tubercles representing the epibranchial spines as in the specimen described by Henderson.

*Locality.* "Mer."

**HYASTENUS BROCKII, De Man.**

*Hyastenus Brockii*, De Man, Arch. Naturg. liii. (1) 1887, p. 221, pl. vii. figs. 1 *a-b*; Henderson, Trans. Linn. Soc., (2) Zool. v. p. 344 (1893).

A single very imperfect dried specimen (♂) appears to agree with De Man's description and figures of this species. The total length is about 15 mm., half of which is taken up by the slender rostral spines. The carapace is narrower and the rostral spines less widely divergent than in the figure. The tubercles on the carapace are only very slightly marked, but the arrangement, so far as can be seen, corresponds with De Man's account. The structure of the orbital region agrees closely with the figure.

*Locality.* "Torres Straits."

*Distribution.* Amboina (*De Man*); Gulf of Martaban (*Henderson*).

**HYASTENUS VERRUCOSIPES (Adams & White). (Plate 2. figs. 23 & 24.)**

*Chorinus verrucosipes*, Adams & White, Zool. Voy. 'Samarang,' Crust. p. 13, pl. ii. fig. 3 (1848).

*Hyastenus verrucosipes*, A. Milne-Edwards, N. Arch. Mus. Paris, viii. p. 250 (1852) (name only).

*Paramithrax verrucosipes*, Miers, Ann. Mag. Nat. Hist. (5) iv. 1879, p. 10 (name only).

This species, which does not appear to have been reobserved since its discovery, is represented in the collection by two female specimens agreeing so closely with the original type specimen of Adams and White as to leave no doubt of their identity. The surface of the carapace is rather more uneven than is represented in the figure given by these authors, and it is slightly more contracted behind the orbital region, so that the postorbital processes appear more prominent. The upper hiatus of the orbit is rather more open in our specimens than in the type, and the rostral spines are distinctly knobbed at the tip. The first pair of walking-legs are relatively longer than in the figure, and the dactyls, especially of the last pair, are longer and more slender. The legs in our specimens do not present the "wart-like tubercles" described by Adams and White; but I am inclined to think, after examining the now somewhat imperfect type specimen, that these tubercles are simply tufts of hair agglutinated together by drying.

As regards the systematic position of this species, Prof. A. Milne-Edwards doubtfully includes it in his list of the species of *Hyastenus*, while Miers incidentally refers to it as a *Paramithrax*. The type specimen in the British Museum is now labelled *Acanthophrys verrucosipes*, and I am informed that this name was given to it by Mr. Miers.

It seems plain, however, that this species cannot be referred to *Paramithrax*, since there is only one hiatus instead of two in the upper margin of the orbit, or, in other words, the spine which, in that genus, intervenes between the supra-ocular hood and the postorbital process is here wanting. The condition of the orbital region is most closely paralleled by Dana's figures of his *Lahaina ovata* (U.S. Expl. Exp., Crust. i. p. 93, pl. ii. figs. 1 *a-c*). The supra-ocular hood is very prominent, having the corners produced and the anterior one acute and curved forwards; the long postocular process is cupped, or rather grooved, along its anterior face for the reception of the eye; the basal antennal joint carries a small spine distally on the ventral surface, and two smaller tubercles in a



line immediately behind it, while a rectangular plate projecting from the outer edge of the joint forms the floor of the orbit. Fairly wide gaps are left between the postocular process and the supra-ocular hood and basal antennal plate in the upper and lower walls of the orbit respectively. Dana's genus is generally regarded as a synonym of *Hyastenus*, and I have accordingly followed Milne-Edwards in adopting that name for the present form, though it differs considerably in the structure of the orbit from those species of *Hyastenus* which I have examined. From *Acanthophrys* it appears to differ in the fact that the inner distal corner of the merus of the third maxillipeds is notched, and the structure of the orbital region is very different from that shown in Milne-Edwards's figure of *A. cristimanus* (Ann. Soc. Ent. France, (4) iv. 1865, pl. v. fig. 3 a).

*Locality.* "Murray Island, channel between reefs, 15-20 fath."

*Distribution.* "Eastern seas" (Adams & White).

#### NAXIA SERPULIFERA (Guérin).

*Naxia serpulifera*, Milne-Edwards, Hist. Nat. Crust. i. p. 313; Haswell, Cat. Austr. Crust. p. 21 (1882); Miers, Rep. Voy. 'Alert,' Crust. p. 196 (1884); Pocock, Ann. Mag. Nat. Hist. (6) v. p. 79 (1890); Ortmann, in Semon's Zool. Forsch. Austral. v., Crust. p. 43 (1894).

A large female specimen (83 mm. in length) of this characteristic Australian species is in the collection.

*Locality.* "Torres Straits."

#### NAXIA TAURUS, Pocock.

*Naxia taurus*, Pocock, Ann. Mag. Nat. Hist. (6) v. p. 70 (1890); Alcock, Journ. Asiatic Soc. Bengal, lxiv. (2) p. 219 (1895); Alcock & Anderson, Illustr. Zool. 'Investigator,' Crust. pl. xxxiii. figs. 5-5 a (1898).

*N. cerastes*, Ortmann, Semon's Zool. Forsch. Austral., v. Crust. p. 43, pl. iii. fig. 4 (1894); Alcock, Journ. Asiatic Soc. Bengal, lxiv. (2) p. 220 (1895); Alcock & Anderson, Illustr. Zool. 'Investigator,' Crust. pl. xxxiii. figs. 2-2 a (1898).

Two male specimens, differing from Pocock's type in the much shorter rostral spines—about 6.5 mm. in a total length of 17 mm.,—with the accessory spinules well in front of the middle of their length. The meral spines, large and conspicuous on the first pair of walking-legs, are all but obsolete on the succeeding pairs. In other respects these individuals do not differ materially from the type specimen. Of the two figures given by Alcock and Anderson our specimens resemble most that named *N. cerastes*, without agreeing precisely with either. It can hardly be doubted, however, that, as Alcock has suggested, *N. cerastes* is merely a variety of *N. taurus*.

*Locality.* "Channels between reefs, Mer, 15-20 fath."

#### TYLOCARCINUS STYX (Herbst).

*Pisa styx*, Milne-Edwards, Hist. Nat. Crust. i. p. 308.

*Microphrys styx*, A. Milne-Edwards, N. Arch. Mus. Paris, viii. p. 247, pl. xi. fig. 4 (1872).

*Tylocarcinus styx*, Miers, Ann. Mag. Nat. Hist. (5) iv. p. 14 (1879); Alcock, Journ. Asiatic Soc. Bengal, lxiv. (2) p. 235 (1895).

A single female specimen. The carapace is a little narrower than in Milne-Edwards's figure, but in other respects the specimen agrees perfectly with this and with Alcock's description.

*Locality.* "Murray Island, reef."

*Distribution.* Red Sea to Fiji.

**PARAMITHRAX (CHLORINOIDES) COPPINGERI, Haswell.**

*Acanthophrys aculeatus*, A. Milne-Edwards, Ann. Soc. Ent. France, (4) v. p. 140, pl. iv. fig. 4 (1865)  
(not *Chorinus aculeatus*, M.-E. Hist. Nat. Crust. i. p. 316).

*Paramithrax Coppingeri*, Haswell, Proc. Linn. Soc. N. S. Wales, vi. p. 750 (1881) \*; Haswell, Cat. Austr. Crust. p. 15.

*Paramithrax (Chlorinoides) Coppingeri*, Miers, Rep. Voy. 'Alert,' p. 192.

*Chlorinoides Coppingeri*, Miers, Rep. 'Challenger' Brachyura, p. 53, pl. vii. fig. 3.

A female specimen, about 6.5 mm. in total length, differs from Miers's figure and from specimens in the British Museum in having the rostral spines short (about one-fourth the length of carapace) and deflexed, and in having the supra-ocular hood deeply cut into three spiniform teeth, the middle one being reflexed at the tip. Miers's figure shows it as obscurely divided into two lobes, but Haswell's original description reads: "upper orbital border with three straight, acute, spinous teeth." Only one spine is present behind the double spines on the cardiac region, as in Miers's description and figure, but a small tubercle represents the second spine which Haswell describes.

The shape of the supra-orbital border in our specimen is very like that shown in Milne-Edwards's figure of *Acanthophrys aculeatus*, which in other respects resembles so closely Miers's figure of *P. Coppingeri* as to leave little room for the doubt which Miers appears to have had as to the identity of the two species. Haswell's name for the species, however, still holds good, since that employed by Milne-Edwards is pre-occupied by the next-mentioned species.

*Locality.* "Torres Straits."

**PARAMITHRAX (CHLORINOIDES) ACULEATUS (Milne-Edwards).**

*Chorinus aculeatus*, Milne-Edwards, Hist. Nat. Crust. i. p. 316.

*Paramithrax (Chlorinoides) aculeatus*, var. *armatus*, Miers, Rep. Voy. 'Alert,' p. 193, pl. xviii. fig. A.  
*Chlorinoides aculeatus*, Miers, Rep. 'Challenger' Brachyura, p. 53; Henderson †, Tr. Linn. Soc., (2) Zool. v. p. 345 (1893).

*Paramithrax (Chlorinoides) aculeatus*, Alcock, Journ. Asiatic Soc. Bengal, lxiv. (2) p. 241 (1895).

A small female specimen appears to find its place among the variations of this species. There are, as usual, five spines on the mid-dorsal line of the carapace, but the spine which in the normal type occupies the middle of the posterior margin appears to be wanting,

\* This reference is given wrongly by Miers in the 'Challenger' Report.

† Henderson's remarks on Miers's variety *armatus* are based on an oversight of the fact that the figure in De Haan's great work, to which he refers, does not represent *P. aculeatus*, though so named on the plate, but De Haan's species *P. longispinus*.

the number being made up by the intercalation of a small spine just in front of the large one on the cardiac region. All the spines of the carapace are distinctly knobbed at the tip. The supra-ocular hood is deeply divided into two teeth, of which the anterior is acute and turned upwards and forwards while the posterior is truncate. The merus of the ambulatory legs bears two spiniform tubercles distally. The rostral spines are strongly divergent and hardly more than one-third of the length of the carapace.

*Locality.* "Torres Straits."

**SCHIZOPHRYS ASPERA (Milne-Edwards).**

*Mithrax asper*, Milne-Edwards, Hist. Nat. Crust. i. p. 320.

*Schizophrys aspera*, A. Milne-Edwards, N. Arch. Mus. Paris, viii. p. 231, pl. x. fig. 1 (1872); Alcock, Journ. Asiatic Soc. Bengal, lxiv. (2) p. 243 (1895); Alcock & Anderson, Illustr. Zool. 'Investigator,' Crust. pl. xxxv. figs. 1, 1 a (1898).

One female and three male specimens, belonging to the typical form of this species as described by A. Milne-Edwards, having only one accessory spinule on each of the rostral horns. The largest male, 26 mm. in length, is still immature, the chelipeds being no longer than the succeeding legs. In the other two males, 17 and 12 mm. long respectively, the carapace is relatively narrower, and in the still smaller female the distance between the extra-orbital spines is hardly less than the greatest width of the carapace. In the small specimens the surface of the carapace between the large tubercles is quite smooth.

*Locality.* "Murray Island."

**CYCLAX SUBORBICULARIS (Stimpson).**

*Cyclomaia margaritata*, A. Milne-Edwards, N. Arch. Mus. Paris, viii. p. 236, pl. x. figs. 2-3 (1872).

*Cyclax suborbicularis*, Alcock, Journ. Asiatic Soc. Bengal, lxiv. (2) p. 245 (1895).

An ovigerous female, 24 mm. in length.

*Locality.* "Murray Island."

*Distribution.* Red Sea to New Caledonia.

**PSEUDOMICIPPA VARIANS, Miers. (Plate 2. figs. 25 & 26.)**

*Pseudomicippe? varians*, Miers, Ann. Mag. Nat. Hist. (5) iv. p. 12, pl. iv. fig. 8 (1879).

*Pseudomicippe? varians*, Miers, Rep. Voy. 'Alert,' Crust. p. 197; Miers, Rep. 'Challenger' Brachyura, p. 68; Ortmann, in Semon's Forsch. Austr., Crust. p. 40.

Three male specimens, agreeing with Miers's types of this briefly described species, and showing the characters assigned by him to the male sex, the gastric region being but little elevated and the rostral spines not perceptibly deflexed.

The only point indicated by Mr. Miers as distinguishing this species from the *P. tenuipes* of A. Milne-Edwards (Ann. Soc. Ent. France, (4) v. p. 139, pl. v. figs. 2, 2 a, 1865) is the character of the sternal surface, which in the last-named species is stated to be "remarquable par l'existence à la ligne de jonction de chaque anneau de crêtes saillantes et légèrement granuleuses." In addition to this, however, certain small differences in

the arrangement of the tubercles on the carapace are apparent on comparing our specimens with Milne-Edwards's account. He states that the gastric region carries a median row of five tubercles flanked by two lateral pairs, but in the figure only four median tubercles are distinctly seen, and this is the case also in our specimens. Milne-Edwards further describes the cardiac region as "marquée de quatre petits tubercules placés de chaque côté de la ligne médiane," but his figure shows two median and two lateral tubercles. In our specimens there is only a bilobed median tubercle in the centre of the cardiac area. Between the main tubercles, and more especially on the branchial regions, the surface of the carapace is in our specimens rather uneven. The rostral spines are stated by Milne-Edwards to be cylindrical: the figure shows them as rather broad and apparently somewhat flattened and having the inner edge obtusely angled about the middle of its length. In the Torres Straits specimens these spines are more slender and cylindrical, tapering only very slightly to the bluntly rounded tip. In the structure of the orbital region, and in the presence of a large tubercle above the orbit external to the base of each rostral spine, our specimens agree closely with Milne-Edwards's species. In spite of the differences above enumerated, the general resemblance between the two species is so considerable that some doubt must still remain as to their distinctness.

Mr. Miers has indicated a doubt as to whether the present species is correctly referred to the genus *Pseudomicippa*. In the type species, *P. nodosa*, Heller (SB. Akad. Wien, xliii. (1) p. 301, pl. i. fig. 3), the rostrum is very strongly deflexed and the anterior angle of the orbit is produced into a long spine, while the basal antennal joint is shaped rather differently, its distal tooth being directed obliquely forwards instead of outwards as in the present form.

As regards the systematic position of the genus, Ortmann points out that it has been wrongly placed among the Malidæ and has no affinity with *Micippa*. He would place it among the Inachidæ, either in the subfamily *Inachinæ* or the *Stenocinopinæ*. Miers, followed by Ortmann, had suggested that the form briefly described by Haswell as the type of a new genus under the name of *Microhalimus deflexifrons* (Proc. Linn. Soc. N. S. Wales, iv. p. 435, pl. xxv. fig. 2, 1879) might be identical with the present species. Alcock, in his classification of the Oxyrhyncha (Journ. Asiatic Soc. Bengal, lxiv. (2) pp. 164 & 166), retains *Microhalimus* and *Pseudomicippa* as distinct genera, placing the former in the "Alliance Inachoida" of his subfamily *Inachinæ*, while classing the latter in the "Alliance Stenocionopoida" of the subfamily *Maininæ*. Alcock does not discuss these genera further, nor does he indicate to which of them the present species should be referred. It seems likely that *P. varians* should be generically separated from *P. nodosa*, and that its most natural position is that which Alcock assigns to *Microhalimus*. Haswell's figure shows, however, that *M. deflexifrons* is at least specifically distinct.

#### MICIPPA PHILYRA (Herbst).

*Micippa mascarenica* (Kossm.), Miers, Ann. Mag. Nat. Hist. xv. p. 7 (1885).

*M. philyra* (Hbst.), Alcock, Journ. Asiatic Soc. Bengal, lxiv. (2) p. 249 (1895).

Three specimens agree very closely with Haswell's description and figures of his

*M. superciliosa* from Torres States (Pr. Linn. Soc. N. S. Wales, iv. p. 446, pl. xxvi. fig. 2, 1879), which is ranked by Alcock as a synonym of this variable and widely distributed species.

*Localities.* "Channel between reefs, Mer"; "Reef, Wyer."

**TIARINIA ANGUSTA, Dana.**

*Tiarinia angusta*, Dana, U.S. Expl. Exp., Crust. i. p. 113, pl. iii. figs. 7 a-b.

*T. spinirostris*, Haswell, Cat. Austr. Crust. p. 28; Ortmann, Zool. Jahrb. Syst. vii. p. 62 (1893).

*T. angusta*, De Man, Zool. Jahrb. Syst. viii. p. 492, pl. xii. fig. 2 (1895).

Our three specimens (2 ♂, 1 ♀) agree closely with Haswell's description of his *T. spinirostris* (which De Man regards as synonymous with Dana's species), save that in the female specimen there are four spines instead of three on the outer margin of each of the rostral horns. De Man figures a specimen with four spines on one side and three on the other, and he describes also a female specimen with only two spines on each side. The carapace of our largest (female) specimen measures 45 mm. in length by 27 mm. in breadth. De Man's largest specimen was 27 mm. long and 14.5 mm. wide. Dana's specimen was only 6 lines long and 2½ lines wide. Haswell gives no dimensions.

*Locality.* "Murray Island."

**LAMBRUS (AULACOLAMBRUS) HOPLONOTUS, Adams & White, var. ?**

*Lambrus hoplonotus*, Adams & White, Voy. 'Samarang,' Crust. p. 35, pl. vii. fig. 3; Miers, Ann. Mag.

Nat. Hist. (5) iv. p. 22 (1879); Miers, Rep. Voy. 'Challenger,' Brachyura, p. 98; Alcock,

Journ. Asiatic Soc. Bengal, lxiv. (2) p. 273 (1895).

A male specimen, 9 mm. in length, is probably to be referred to "this protean species," as Miers calls it. It differs considerably from the figure of Adams and White, the whole anterior part of the carapace being much narrower and more produced, and the rostrum projecting well in front of the orbits. There is a slight postorbital constriction, followed by a sharp hepatic tooth, which is longer than the succeeding spiniform teeth of the lateral margins. The granules on the surface of the carapace are acute and spiniform. Our specimen agrees pretty closely with some referred by Mr. Miers to his variety *longiocularis*, which "is best distinguishable by the subspiniform tubercles of the branchial regions" ('Challenger' Brachyura, p. 99), the greater protrusion of the eyes being, I believe, quite an accidental circumstance.

*Locality.* "Torres Straits."

**LAMBRUS (PARTHENOLAMBRUS) CALAPPOIDES, Adams & White.**

*Parthenope calappoides*, Adams & White, Rep. Voy. 'Samarang,' Crust. p. 34, pl. v. fig. 5.

*Lambrus (Parthenolambrus) calappoides*, Alcock, Journ. Asiatic Soc. Bengal, lxiv. (2) p. 275 (1895).

Our single specimen, a male, is only about 7.5 mm. in length, and the points of difference from the figure of Adams and White are probably due to its small size. The surface is rather smoother, the incision marking off the hepatic prominence posteriorly is hardly perceptible, and the posterior edge of the carapace is more regularly crenated.

*Locality.* "Channel between reefs, Mer."



LAMBRUS (PARTHENOLAMBRUS) CONFRAGOSUS, n. sp. (Plate 3. figs. 27 & 28.)

*Description of female.* Carapace roughly triangular in outline, about as long as broad. Rostrum truncated and considerably deflexed. Hepatic regions projecting in the form of a vertically compressed, narrow, bluntly pointed tooth. In front this tooth is defined by a deep notch separating it from the postorbital angle, and behind a shallower excavation marks it off from the convex, crenated, lateral margin. The postero-lateral corners are produced into short, blunt spines. The posterior margin is irregularly toothed, with a marked excavation on either side a little way from the outer end and an obtuse median angle, which projects well beyond the line joining the postero-lateral corners. The surface of the carapace is very uneven and irregularly granulated and pitted. The gastric and cardiac regions rise each into a short, blunt spine, and a smaller spine or large tubercle lies between the cardiac spine and the posterior margin. The branchial regions are inflated, topped with oblique crests of granules, and separated from the median regions of the carapace by well-marked grooves, which sink into deep fossæ on either side of the gastric and cardiac regions.

The chelipeds are very heavy, slightly unequal, and about one and a half times the length of the carapace. The merus is irregularly toothed along its anterior and posterior borders. The hand bears on its outer (or upper) margin two thin, rounded, cristiform lobes, of which the larger is close to the proximal end. The upper surface carries an oblique and irregularly toothed crest, and is elsewhere unevenly granulated. The fingers are rather less than half the length of the palm, and the dactylus is toothed and granulated on its outer (or upper) margin near the base. The ambulatory legs are much compressed, with the upper and lower margins of the joints serrate.

Length of carapace 15 mm.

A second specimen, only 8 mm. long, probably belongs to the same species. The carapace is a little longer than broad, the rostrum is tridentate and even more strongly deflexed than in the specimen above described. The hepatic prominences, though very well-marked, are not so much compressed and dentiform. The surface of the carapace is smoother, and the crenations of the lateral margins less numerous. The chelipeds are rather more slender, and there is only one cristiform lobe on the outer edge near the base.

The species described above, which I suppose to be new, resembles in general form the *L. tarpeius* of Adams and White, but differs from it in the much more rugged surface of the carapace, in the compressed dentiform shape of the hepatic prominences, and in the armature of the chelipeds, which in the last-named species lack the flattened cristiform lobes on the outer margin of the hand. Many species, however, of this extensive genus are known to vary within wide limits, and it is possible that a larger series of specimens than has been accessible to me would unite the present form with one or other of the species already described.

*Locality.* "Channel between reefs, Mer."

**HAPALOCARCINUS MARSUPIALIS**, Stimpson. (Plate 3. figs. 29–40.)

*Hapalocarcinus marsupialis*, Stimpson, Proc. Boston Soc. Nat. Hist. vi. 1856–59, p. 412; Semper, 'The Natural Conditions of Existence as they affect Animal Life' (London, 1881; Internat. Sci. Series), pp. 216 *et seq.*, fig. 64 c.

*Description of female.* The carapace is soft and membranous, depressed, broadly oval in outline and truncated in front and behind. The breadth is equal to or a little less than the length. The front is slightly deflexed, obscurely tridentate, the median tooth being sharp and separated by a shallow concavity on either side from the rounded lateral corners. There are no true orbits, the space occupied by the eye being quite undefined above and externally, while below the eye rests directly on the everted anterior margin of the buccal frame. The lateral margins of the carapace are rounded off dorso-ventrally and evenly arcuate from before backwards. The posterior margin is concave and is about three-fifths as long as the anterior margin. The surface of the carapace is perfectly even, without any perceptible furrows, and is smooth except for a few minute and widely-scattered setæ.

The abdomen consists of seven distinct segments, of which the first is partly concealed under the posterior margin of the carapace. The first three segments are visible from above, and are hardly more than half the width of the carapace. The remaining four segments are bent under the body, and form a broad oval plate about equal in size to the carapace. The middle part of this plate, formed by the terga of the four segments, is of somewhat firm consistency and is surrounded by a wide membranous border, which at the sides is folded inwards to form the lateral walls of the capacious egg-pouch. The surface of the abdomen, like that of the carapace, is beset with minute scattered setæ.

The ocular peduncles are relatively large, subconical, not lying in distinct orbits. The corneal surface is faceted, but, in our specimens, devoid of pigment. The antennules are large and exserted, there being no fossettes for their reception. The basal joint is produced externally into a large conical process directed obliquely forwards and terminating in a stout spine. The two succeeding joints are stout, cylindrical, and subequal in length, the distal one carrying the two rudimentary flagella, each consisting of a few joints and clothed with numerous long setæ. The antennæ consist of five joints, of which the first is broad and triangular and the succeeding joints narrow, cylindrical, and successively diminishing in diameter, the last being hardly thicker than the long seta which springs from its tip. The buccal area is very large, extending across the whole width of the carapace in front. Its anterior margin is sinuous, curving forwards on either side below the eye, and taking the place usually occupied by the inferior margin of the orbit. The median part of the buccal margin approaches so closely to the base of the antennules that an epistome can hardly be said to exist. The third maxillipeds do not nearly cover the buccal cavity, and are widely separated from each other at the base by a semicircular area of the sternum. The ischium is flattened, subtriangular in shape, widening gradually from a narrow base, and having its antero-internal angle produced forwards, rounded, and fringed with setæ. The merus is articulated at the outer end of the distal

margin of the ischium, and is less than half the width of the latter, hardly wider than the succeeding joints, and but little flattened. The exopod is rudimentary, being a simple lobe about half the length of the ischium. The epipod is well-developed. The second maxillipeds have the basal part of the exopod much expanded. In the first maxillipeds, also, the same part is very stout and much stronger than is usual in this appendage, while the inner lobe or endopod is small and subtriangular. The chelipeds are rather stout, about twice the diameter of the succeeding legs, and smooth save for scattered setæ similar to those on the carapace. The merus has a small spine near the distal end of the inner margin. The hand is not much thicker than the preceding joints. The palm is less than twice as long as broad, nearly twice as long as the fingers. The dactylus has a single tubercle on its inner edge. The walking-legs are not at all concealed by the carapace. The first three pairs are about equal in length to the chelipeds and the last pair is a little shorter. The dactyli are strong and curved, and bear a low tooth on the inner edge near the tip. The legs bear scattered setæ, which are larger and more numerous than are those on the body. The abdominal appendages are reduced to three pairs, corresponding to the second, third, and fourth abdominal somites. They are uniramous with the exception of the first, which carries on the outer side near the base a small unjointed appendage which appears to represent the exopod.

The female generative apertures are crescentic in form, and are situated on the sternum, far apart from each other, close to the bases of the third legs.

The dimensions of our two specimens are as follows:—

Length of carapace .....	2·6 mm.	2·7 mm.
Breadth „ .....	2·4 „	2·7 „
Length of cheliped.....	.....	3·0 „
„ chela .....	.....	1·3 „
„ fingers .....	.....	·5 „
„ last leg .....	.....	2·6 „

Stimpson's brief description applies very well, on the whole, to the specimens examined by me. The most serious discrepancy is that the exopod of the third maxillipeds is described as "slender and palpigerous." It seems quite possible, however, that in examining the entire animal the rudimentary exopod of this appendage may have been overlooked, and the more conspicuous exopod of the second maxilliped may have appeared to belong to the third. The antennules are stated to be "very short and minute," but as they are said to be "placed at the inner angle of the orbit," it seems not unlikely that these epithets should be transferred to the antennæ, to which they are more applicable. Some other less important differences, such as the description of the front as "straight," may reasonably be attributed to imperfect observation. On the other hand, the description of the general shape, the large abdomen, the large buccal area occupying nearly the whole breadth of the carapace, the third maxillipeds with "the ischium large and dilated within, while the merus is very small and slender like the last three joints," and several other details can apply to no other crustacean, and leave no doubt that we are dealing with Stimpson's species.

So far as I can discover, no further description of this remarkable form has been published. Semper gives a figure of it, but it is on too small a scale to be of much use. It represents the carapace as proportionately broader than in our specimens. All the recorded specimens have been females.

The peculiar habitat of this Crab was unknown to Dr. Stimpson, who states that his specimens were found "clinging to the branches of living madrepores at the depth of one fathom in the harbour of Hilo, Hawaii."

Ehrenberg had long before noticed certain deformities on corals caused by the presence of crustacea, and had compared them to the galls formed by plants. In his work on the Corals of the Red Sea he writes of the species *Seriatopora subulata*, Lamk.:—"Paguri parvi (*P. coralliophilos*) domicilia in ramis efflorescentibus sibi parant, et veras gallas fere eliciunt, quales plantæ gerunt" (Beitr. z. Kennt. Korall. roth. Meeres, p. 123). I am not aware that Ehrenberg's "*Pagurus*" has since been recognized, or that any other Pagurid has been found inhabiting coral-galls, so that it is possible that Ehrenberg's remarks may really refer to the present species\*. Be this as it may, Verrill was the first to definitely associate these coral-"galls" with Stimpson's *Hapalocarcinus*. In a paper on "Remarkable Instances of Crustacean Parasitism" (Amer. Journ. Sci. (2) xliv. 1867, p. 126) he writes:—"Another peculiar mode of parasitism I have observed in a singular crustacean (*Hapalocarcinus marsupialis*, Stimpson) from the Sandwich Islands. This creature lodges itself among the slender branches of a coral (*Pocillopora cæspitosa*, Dana), and causes, probably by its incessant motions, the branches to grow up and surround it on both sides by flat expansions of coral terminating in digitations which often interlock above, leaving openings between them suitable for the uses of the parasite but usually too small to allow of egress. Most specimens of the corals of this species sustain one or more and often numerous examples of these curious enlarged bulbs among the branches." In a subsequent paper "On the Parasitic Habits of Crustacea" (Amer. Nat. iii. 1869, p. 239), Prof. Verrill adds that he had "observed similar cavities on *Pocillopora elongata* from Ceylon, which are probably made by another species of the same genus." In his "Synopsis of the Polyps and Corals of the North Pacific Exploring Expedition" (Proc. Essex Inst. vi. (1868) 1870, p. 91), the same writer records the occurrence of galls on most of the specimens of *Pocillopora cæspitosa*, Dana, from the Hawaiian Islands, and he also writes of *P. brevicornis*, Lamk.:—"One specimen has a bulb similar to those made by *Hapalocarcinus marsupialis*, but belonging probably to another species of the same genus, since it differs considerably in form. The aperture is closed except a few small openings above."

In the general account of his researches in the Philippine Islands (Zeit. wiss. Zool. xiii. 1863, p. 560), Semper has a note on a small "*Porcellana*" which he found living in cavities in a "millepore." In his work on 'The Natural Conditions of Existence as

\* I learn from Mr. R. Kirkpatrick, who has been kind enough to find the above quotation for me, that Künzinger refers to Ehrenberg's observations, and gives a figure of the galls on the same species of coral (which he refers to *S. spinosa*, M.-E. & H.) without, however, giving any details as to the parasite (Korall. roth. Meer. ii. p. 72, pl. vii. fig. 15).

they affect Animal Life' (1881) this Crab is identified with the present species, and a fuller account is given of the "galls" formed by it. These were found on the corals *Sideropora digitata* and *S. palmata* and on species of *Seriatopora*. He describes the formation of the gall by the growth of two broad flattened branches, and notes that the shape differs according to the species of the coral. "In the *Seriatopora* both the twigs are leaf-shaped and beset with more or less numerous offshoots terminating in sharp spines. In the more solid *Pocillopora* the twigs also have spines, but they are more massive. Finally, in *Sideropora* spines are wholly absent, and the two twigs between which the crab lives are altogether more massive." He describes the gradual closure of the gall by concrescence of the edges, "till at length only two fissures, more or less wide, are left, which plainly show, by their position opposite to each other, that it is through them that the current for respiration passes: one fissure serves for the influx, the other for the exit, of the water;" and reasons are given for believing that these fissures are kept open owing to the current of water checking the growth of the coral so long as the crab remains alive.

Semper states that a *Hapalocarcinus*, "it would seem identical in species," occurs at Réunion (p. 281), but I can find no other record of its occurrence there. He also mentions (pp. 217 & 453) certain observations by Graeffe, but no reference is given, and I have failed to trace the source from which he quotes\*.

Bassett-Smith† has described galls formed by a crab on *Seriatopora imbricata*, B.-S., from the Tizard Bank in the China Sea. The crab is not described, but it probably belonged to the present species.

Hickson‡ has described and figured galls on a *Millepora* containing a crab which he assumes to be *Hapalocarcinus*. The galls are unlike those described by the authors quoted above, being inflated bulbs with a single, wide, terminal aperture.

The series of galls examined by me are formed on a species of *Seriatopora*§, and the mode of growth agrees well with the descriptions of Verrill and Semper. The earliest stage is represented by a specimen (fig. 38) in which the gall is beginning to be formed at the point of bifurcation of a branch. A broad palmate process, slightly concave internally,

\* As certain passages from Semper's work have recently been quoted, without correction, by Hickson, it may not be superfluous to point out that the English edition of this work (I have not been able to consult the German edition) abounds in typographical and other errata. Thus, on p. 216, the date of Stimpson's paper is given as 1837 (Stimpson was born in 1832) instead of between 1856 and 1859. On p. 217 it is stated that the present species was "discovered in the Pacific Ocean by Dana in the course of his great voyage under the command of Wilkes." As a matter of fact, the specimens were collected (no doubt by Stimpson himself) during the U.S. North Pacific Surveying Expedition under Capt. John Rodgers. The incidental references to the carrying of the young in the brood-pouch (p. 217) and to the course of the respiratory current (p. 219) are our only authority for believing that *Hapalocarcinus* differs in these respects from the majority of the Brachyura. In the explanation of fig. 65 (p. 218) *Sideropora hystrix* should probably read *Seriatopora hystrix*.

† Ann. Mag. Nat. Hist. (6) vi. 1890, p. 364.

‡ Bull. Liverpool Mus. i. nos. 3 & 4, pp. 81-82, plate.

§ Prof. F. Jeffrey Bell, who has kindly examined my specimens, informs me that their fragmentary nature renders an exact determination difficult, but that they seem to approach most closely to *S. elegans*, M.-E., though differing from it in certain characters.



forms one side of the cavity in which the parasite was lodged, the other side being formed by an expansion of the opposed part of the main branch, at the sides of which lobate projections are beginning to develop. A considerably more advanced gall is shown in fig. 39. Here the gall is terminal in position and is roughly lenticular in form, the two digitate lobes which compose it being perforated by fissures and only touching each other here and there at the edges. A still older gall (fig. 40), occupying a lateral position on a branch, is closed except for two or three very small apertures at or near the margin. These apertures are not placed regularly opposite to each other as Semper states. On the outer surface of the gall the calicles are rather smaller than those on the normal branches and are not arranged like them in series, but appear to be otherwise well developed. On the inner surface of the gall the calicles, as Semper states, are small, shallow, and have the septa only feebly developed. They are also in some parts distorted and drawn out to an elliptical outline, but this distortion does not appear to be definitely related to the marginal apertures of the gall as described by Semper, who attributes it to the action of the current of water caused by the crab. Semper also found on the inner surface "very distinct scars, which are evidently produced by continual scratching in one spot," and he concludes that the crab usually remains in one position within the gall. Such scars are not visible in our specimens. In the older galls the outer surface rises into rounded, irregularly placed swellings and short branches, as if the coral were about to resume the normal habit of growth disturbed by the intrusion of the parasite.

From Semper's earlier note we gather the not uninteresting detail that the polypes on the inner surface of the gall are colourless.

As regards the further habits and life-history of *Hapalocarcinus* we have no information. The fact that each gall is inhabited by a solitary female, while the male is as yet unknown, would seem to indicate that both sexes are at first free-living, and that it is only after impregnation that the female becomes imprisoned in a gall. The fact that the youngest gall observed is of ample size to contain a full-grown *Hapalocarcinus* tends to confirm this suggestion.

As regards the systematic position of *Hapalocarcinus*, we have to note in the first place its close affinity with the *Cryptochirus coralliodytes* of Heller ("Beitr. z. Crust. Fauna d. roth. Meeres," SB. Akad. Wien, xliii. (1) 1861, p. 366, pl. ii. figs. 33-39). As Semper has shown ('Animal Life,' pp. 217, 221-223)\*, *Cryptochirus*, like *Hapalocarcinus*, is parasitic on living corals. In this case, however, no closed "galls" are formed, the crab living in massive corals (ex. *Goniastrea*,) at the bottom of a funnel-shaped depression, due to an arrest of the upward growth of the coral. The affinity between the two genera is most clearly shown by the third maxillipeds, which in both cases are peculiar in having the merus-joint very narrow and the exopod rudimentary. The structure of the facial region is somewhat similar in both, the antennules not being retractile into fossettes, while the antennæ are very small and the orbits ill-defined. The abdomen of the female in both genera is much enlarged, but in *Cryptochirus* it lies

\* Semper's figure of *Cryptochirus* differs considerably from those given by Heller. He states, however, that the Philippine form "appears to be in no respect specifically different" from that found in the Red Sea (*op. cit.* p. 281).

wholly behind the carapace, and is bent upon itself so as to form a deep pouch, open only in front, while in *Hapalocarcinus* it is flexed under the body in the manner usual among the Brachyura. Among other differences the orbits of *Cryptochirus* are defined externally by a strong tooth, and the basal joint of the antennules presents a serrate edge anteriorly where that of *Hapalocarcinus* has only a stout dentiform lobe.

In describing *Hapalocarcinus*, Stimpson noted its resemblance to *Pinnotheres* in the large size of the abdomen and the softness of the integument, and he stated that its systematic position was probably between *Pinnotheres* and *Hymenosoma*. Apart from the two points mentioned, there seems to be little in the characters of the species as now described to suggest affinity with the Pinnotheridæ, while the third maxillipeds are widely different in type from anything found in that group.

Heller expressed no opinion as to the systematic place of his *Cryptochirus*.

A. Milne-Edwards, however, has described under the name *Lithoscaptus paradoxus* (in Maillard's 'Notes sur l'Ile de la Réunion,' 2<sup>m</sup> éd., 1863, ii. Annexe F, pp. 10-12), a form which, as Paulson has already pointed out, is in all probability identical with, or closely allied to, Heller's species. This genus was regarded by Milne-Edwards as representing a new family, "Lithoscaptes," among the "Brachyures anormaux." He writes, "par sa région céphalothoracique le Lithoscapte se rapproche des Ranines plus que tout autre groupe de Décapodes." Special resemblances to the Raninidæ are said to exist in the structure of the antennal region and in the shape of the thoracic sternal region, which is broad in front but much contracted between the bases of the last two pairs of legs. It is not clear, either from Milne-Edwards's or from Heller's accounts (supposing the two genera to be identical), in what way the antennal region resembles that of the Raninidæ, while the thoracic sternum is not contracted posteriorly, at all events in the female *Hapalocarcinus*. Heller describes the sternum of *Cryptochirus* as "ziemlich breit, länglich oval." The third maxillipeds are said by Milne-Edwards to resemble a little those of *Remipes*, but this resemblance appears to consist merely in the absence of a conspicuous exopod. Milne-Edwards describes the abdominal appendages as uniramous and as existing on the first four somites. According to Heller there are only three pairs, and this agrees with our examination of *Hapalocarcinus*.

Paulson refers *Lithoscaptus* (= *Cryptochirus*) to the Pinnotheridæ, establishing for its reception a new subfamily, which he designates *Crypochirinæ* and defines as follows:—"Cephalothorax convex, almost twice as long as broad. Inner antennæ without fossettes and lying longitudinally. Basal portion of the outer antennæ free. Third joint of the outer maxillipeds considerably shorter than the second. Openings of the female sexual organs on the sternum" ('Crust. Red Sea,' Kiev, 1875, p. 72).

While the characters of *Hapalocarcinus*, as now described, show clearly that it must stand alongside *Cryptochirus*, they give little help towards settling the place of the two genera in the system. The position of the female genital apertures shows that they must be placed among the true Brachyura, although there are some curious resemblances to individual genera of the Anomura. Thus the endopod of the third maxillipeds

resembles somewhat that of *Porcellana*, while the rudimentary exopod suggests a comparison with the *Hippidea*. The number and uniramous condition of the abdominal appendages also agree, except for the absence of the sixth pair, with the last-named group. These resemblances, however, are balanced by numerous important differences, so that even were we to set aside the evidence of the genital openings, it would be impossible to place the genera in any of the groups of Anomura. On the other hand, the characters of the third maxillipeds and of the abdominal appendages and the greatly enlarged buccal area are unlike anything found among the Brachyura. The resemblance to the Pinnotheridæ appears to be quite superficial.

The characters usually relied upon to distinguish the various divisions of the Brachyura have been in this case apparently so profoundly modified by the parasitic habit of life, that we can only regard these two genera as forming a family for the present *incertæ sedis*, for which the name Hapalocarcinidæ will have to replace Milne-Edwards's "Lithoscaptæ," the latter being based on a synonym of *Cryptochirus*.

*Locality.* "Torres Straits."

*Distribution.* *Hapalocarcinus* is recorded by name from Hawaii (*Stimpson, Verrill*), the Philippines, and (?) Bourbon (*Semper*). Coral-galls, possibly due to this species, are known from the Red Sea (*Ehrenberg, Klunzinger*), Ceylon (*Verrill*), and the China Sea (*Bassett-Smith*).

## EXPLANATION OF THE PLATES.

### PLATE 1.

- Fig. 1. *Pilumnus cristipes*, n. sp., ♀ (enlarged).  
 2. " " " Cephalic region from below.  
 3. " " " Right chela.  
 4. *Cryptocnemus Haddoni*, n. sp., ♀. Dorsal view, × 6.  
 5. " " " Ventral view.  
 6. " " " Lateral view.  
 7. " " " Third maxilliped, inner face.  
 8. " " " Chela.  
 9. *Palicus Jukesii* (White), ♂, × 5.  
 10. " " " Cephalic region from below.  
 11. " " " Abdomen.  
 12. " " " Second walking-leg from below.  
 13. " " " First abdominal appendage.

## PLATE 2.

Fig. 14. *Palicus Whitei* (Miers), ♀, × 3½.

- 15. " " " Cephalic region from below.
- 16. " " " Abdomen, ♀.
- 17. " " " Abdomen, ♂.
- 18. " " " Second walking-leg from below.
- 19. " " " First abdominal appendage, ♂.
- 20. *Palicus serripes* (Alc. & Aud.), ♀, × 4.
- 21. " " " Cephalic region from below.
- 22. " " " Second walking-leg from below.
- 23. *Hyastenus verrucosipes* (Ad. & Wh.). Dorsal view (setæ omitted), × 5.
- 24. " " " Cephalic region from below.
- 25. *Pseudomicippa varians*, Miers, × 4.
- 26. " " " Cephalic region from below (setæ omitted).

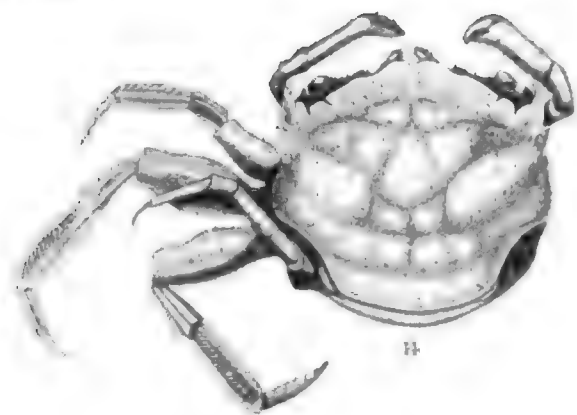
## PLATE 3.

Fig. 27. *Lambrus confrago* n. sp., × 2½.

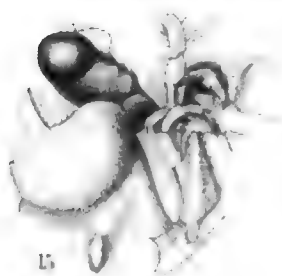
- 28. " " " Outline from side.
- 29. *Hapalocarcinus marsupialis*, Stimpson, ♀. Dorsal view, × 13.
- 30. " " " Ventral view.
- 31. " " " Ventral view of cephalic region.
- 32. " " " Antennæ and antennules.
- 33. " " " First maxilliped.
- 34. " " " Second maxilliped.
- 35. " " " Third maxilliped.
- 36. " " " Chela.
- 37. " " " Dactylus of last walking-leg.
- 38. Branch of *Seriatopora* sp., showing at \* beginning of "gall" formed by *Hapalocarcinus*.
- 39. A more advanced "gall," still widely open at edges.
- 40. A "gall," closed all round except for a few small apertures marked \*.







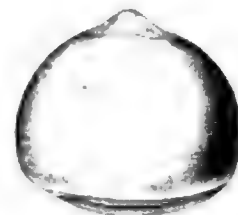
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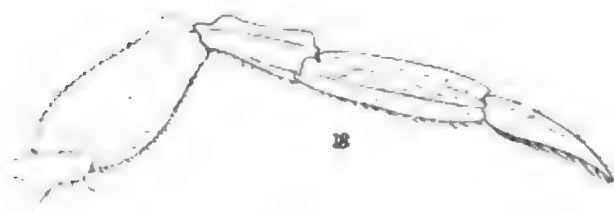
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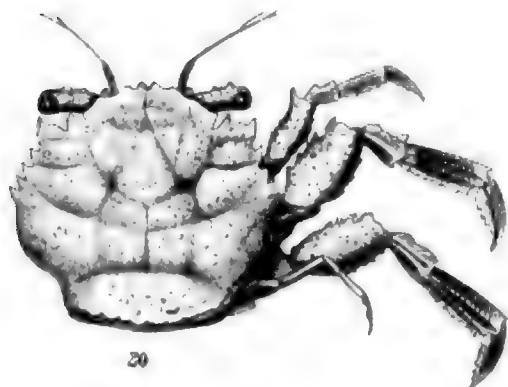
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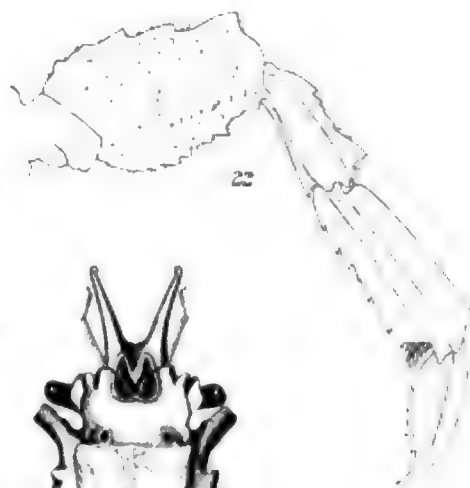
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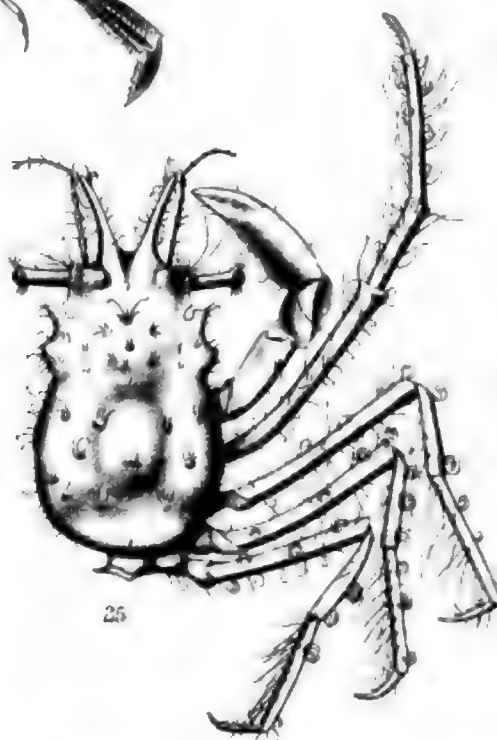
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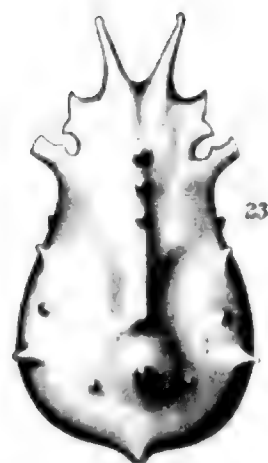
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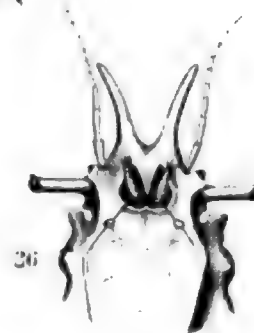
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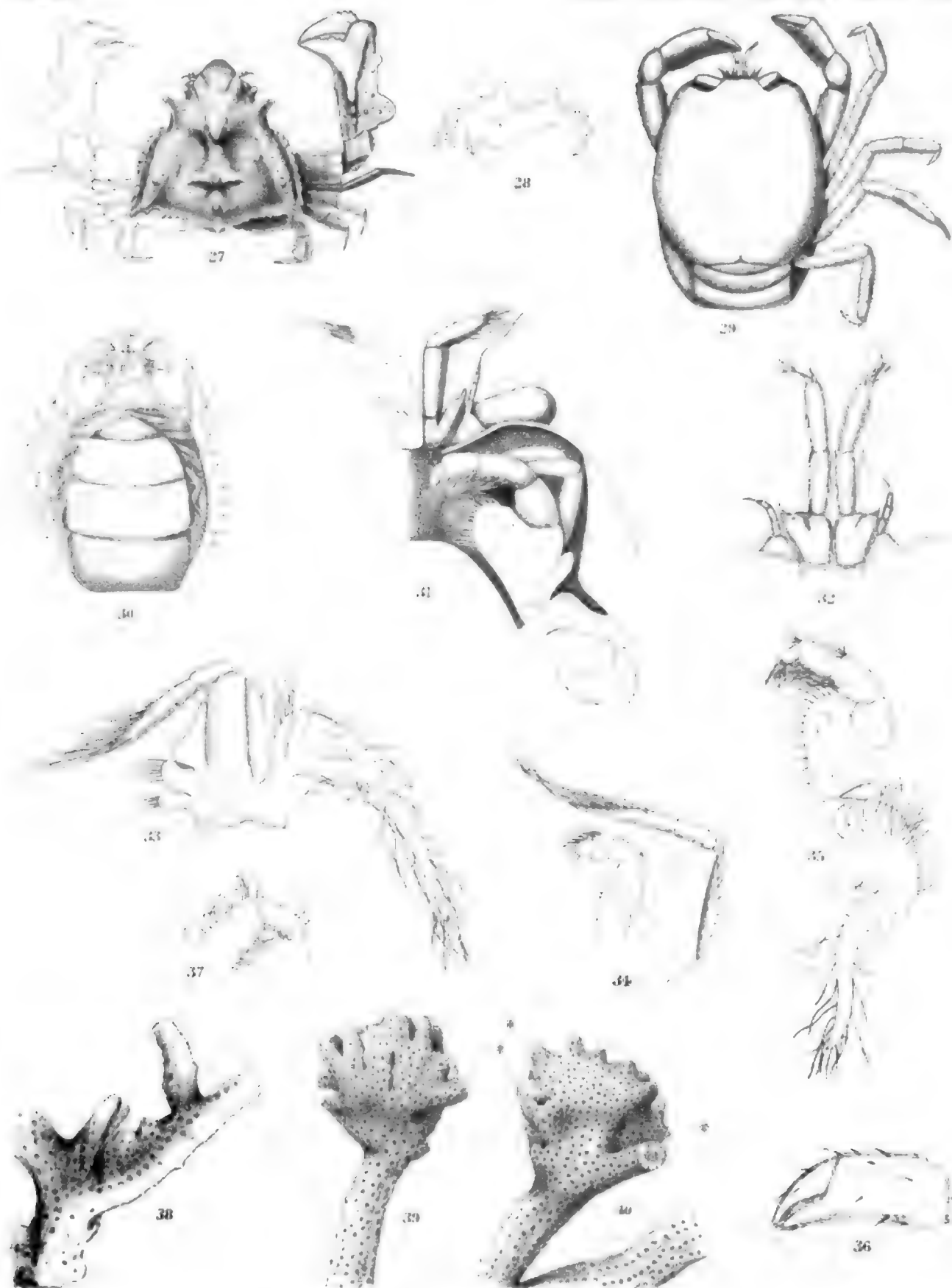


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W.T.C. del.  
M.P. Parker lith.

BRACHYURA FROM TORRES STRAITS

Geo. West & Sons 1792p



W.T.C. del.  
M.P. Parker lith.

BRACHYURA FROM TORRES STRAITS.

See West & Renss.

II. *Report on a Collection made by Messrs. F. V. McCONNELL and J. J. QUELCH at Mount Roraima in British Guiana. (Communicated by Professor E. RAY LANKESTER, D.C.L., F.R.S., Director of the Natural History Museum.)*

(Plates 4-6.)

Read 1st February, 1900.

FOR some years past the British Museum has received many interesting collections made by Mr. F. V. McConnell and Mr. J. J. Quelch during their various expeditions into the interior of British Guiana. On the last occasion the explorers succeeded in reaching the summit of Mount Roraima, and I have much pleasure in forwarding the accompanying descriptions of the new species obtained during the expedition, all of which have been worked out by members of the staff of the Zoological Department of the British Museum, excepting the Crustacea, which have been dealt with by Dr. de Man.

Mr. McConnell has kindly sent me the following note:—"The specimens were obtained by Mr. J. J. Quelch and myself on our second expedition to Roraima in August, September, and October, 1898. The route taken on this occasion was by the Mazaruni and Curubung rivers to the Falls of Macrobah, a boat-journey of twenty days, and thence by land to a point on the Upper Mazaruni where that river flows at a height of 1300 feet. Small bark-canoes were here obtained, and after three days' journey up the Cako and Aruparu we arrived at the commencement of the trail to Roraima. With the exception of the last twenty miles, the whole journey, which occupied forty days, lay through thick forest.

"Mount Roraima (8700 feet) is formed by a sloping base, surmounted by a rectangular mass, fifty-four square miles in area, with perpendicular walls 2000 feet in height. On the south-west, part of the wall has slipped, and lies diagonally across the face of the upper part of the mountain. By following the ledge so formed the summit can be reached without serious difficulty."—E. RAY LANKESTER.

**MAMMALIA.**

By W. E. DE WINTON, F.Z.S.

## Order RODENTIA.

**RHIPIDOMYS MACCONNELLI, sp. n.**

The general colour of the entire upper surface rich golden brown; the fur is very soft, from 11 to 12 millimetres in length, dull black for the greater part of its length with bright red golden tips; the slightly longer straight hairs have black tips; the lower surface is dirty white or drab, the fur being dull black with whitish tips, with no line of demarcation between the colours of the upper and lower surfaces. The ears are large, round, and naked, almost black in colour. The hands and feet dirty white, rather darker on the upper surfaces, almost naked. Whiskers long, reaching beyond the shoulders. The tail is brown, only very slightly paler beneath, practically naked, the very minute hairs in no way hiding the scales; at the extreme tip there is a long pencil of hairs about 10 millimetres long, but no bushy hairs on the sides.

Upper incisors dull orange, rather darker than those of the lower jaw.

Measurements taken from the specimen in alcohol:—Head and body 95 millim., tail 147, hind foot 24·5, ear 17.

Skull—greatest length 26·5; greatest breadth 14·5, across brain-case 12·7; narrowest interorbital constriction 4·6; length of nasals 9·1; basal length 22·6; back of incisors to back of palate 11·5; incisive foramina 5·9 × 2·5; diastema 7; length of molar series 5; width outside first molar 5·5, outside last molar 5·9; mandible, tip of incisors to coronoid process 12, to condylar process 17·8, to angle 17·3.

The type and only specimen was found on the summit of Roraima, Demerara, and has been presented to the Museum by Messrs. McConnell and Quelch.

The skull is fragile and transparent, with large, smooth brain-case; the zygomata are very thin and weak, expanding very little beyond the sides of the head in the squamosal region only. The molars are set in almost parallel rows; the auditory bullæ are very small; the foramen magnum is very large, the surrounding bones very thin, especially the basioccipital condyles.

This new *Rhipidomys* is of much the same size as *R. microtis*, Thos., from Colombia, but the colour is distinct, being much darker above, while the underparts are greyish with dark bases to all the fur instead of being pure white; then the ears of the new species are large, while those of the Colombian species are very small. The tip of the tail may or may not be distinct, for the end of the tail of the type of *R. microtis* appears to me to be wanting.

The broken state of the skull of *R. microtis* excludes the possibility of a fair comparison being made, but in the dentition the two species seem very similar.

## BIRDS.

By R. BOWDLER SHARPE, LL.D., F.L.S.

(Plate 4.)

FROM the summit of Roraima Mr. McConnell brought several specimens of a *Zonotrichia* quite distinct from the ordinary *Z. pileata* which is found over the greater part of Central and South America. It is a larger and darker bird, much greyer, and with the rump and flanks dark grey instead of brown. I propose to call it after Mr. McConnell, who has done so much for the collections of the British Museum.

*ZONOTRICHIA MACCONNELLI*, sp. n.

Similis *Z. pileata*, sed major, obscurior, uropygio et hypochondriis saturatè griseis, nec brunneis distinguenda. Long. tot. 5·8 poll., culm. 0·6, alæ 2·8, caudæ 2·35, tarsi 0·9.

*Hab.* Summit of Mount Roraima.

## EXPLANATION OF PLATE 4.

Fig. 1. *Zonotrichia Macconnelli*.2. „ „ *pileata*.

## REPTILES.

By G. A. BOULENGER, F.R.S.

(Plate 5. figs. 1-2.)

1. *ANOLIS FUSCO-AURATUS*, D'Orb.

This and most of the following Reptiles and Batrachians were obtained at the base of the mountain, at an altitude of about 3500 feet. *Prionodactylus leucostictus* and *Oreophrynella Quelchii* are from the summit (8600 feet).

2. *CENTROPYX CALCARATUS*, Spix.3. *CENTROPYX STRIATUS*, Daud.4. *NEUSTICURUS RUDIS*, sp. n. (Plate 5. figs. 1-1 c.)

Snout rather short, pointed; canthus rostralis strong; ear-opening as large as the eye-opening; transparent disk of lower eyelid composed of five pieces. Rostral rather large, the portion visible from above nearly half as long as the frontonasal, which is longer than broad; a pair of præfrontals; a single frontal; a pair of frontoparietals, followed by five shields in a row; occipital region covered with small irregular shields; three



large supraoculars, preceded by a small fourth and two or three granules; nostril pierced in a single nasal, which, like the loreals and suboculars, is in contact with the upper labials; latter, seven in number, fourth largest; four lower labials; chin-shields, one anterior and two pairs. Gular scales smooth, smallest on a zone connecting the ears; collar bordered by six plates. Nape and back covered with small keeled scales intermixed with large, oval, sharply keeled tubercles, disposed very irregularly, but avoiding the vertebral line; smaller tubercles on the sides. Ventral plates rounded posteriorly, imbricate, in 8 or 10 longitudinal and 28 transverse series; the plates of the four median rows subequal, about as long as broad. Three slightly enlarged præanal plates, forming a triangle. 18-20 femoral pores. Tail feebly compressed, with the pair of dorsal keels, formed by enlarged tubercles, feebly developed. Uniform blackish brown above, whitish beneath.

Total length .....	183 millim.	From end of snout to vent ...	59 millim.
Head .....	14 "	Fore limb .....	19 "
Width of head .....	8.5 "	Hind limb .....	27 "
From end of snout to fore limb...	23 "	Tail .....	124 "

A single specimen (♂) from the foot of Mt. Roraima, 3500 feet.

5. *PRIONODACTYLUS LEUCOSTICTUS*, sp. n. (Plate 5. figs. 2-2 c.)

Snout short, obtusely pointed; ear-opening a little smaller than the eye-opening. Frontonasal single, a little broader than long; præfrontals well developed, forming a median suture; interparietal large, hexagonal, larger than the parietals; two pairs of occipitals; four supraoculars; nostril pierced in a single nasal; no loreal; six upper and five lower labials; chin-shields very large, one anterior and four pairs, the first two forming a suture, the two others separated on the median line by granules; two longitudinal rows of large transverse gular shields; five collar-shields. Dorsal scales hexagonal, strongly keeled; lateral scales small, roundish, smooth; 26 scales, including the ventrals, round the middle of the body; 29 scales from occiput to base of tail. Ventrals large, in 8 longitudinal and 19 transverse series. Four large præanal shields, forming a cross. 6 femoral pores on each side (♀). Tail above with hexagonal keeled scales, beneath with tetragonal smooth scales. Black above and beneath; each scale or shield with one to three white dots, these dots larger on the ventral shields; chin white.

Total length .....	127 millim.	From end of snout to vent ...	50 millim.
Head .....	10 "	Fore limb.....	13 "
Width of head .....	6 "	Hind limb .....	19 "
From end of snout to fore limb...	19 "	Tail .....	77 "

A single specimen (♀) from the summit of Mt. Roraima, 8600 feet.

6. *LACHESIS LANCEOLATUS*, Lacép.

**BATRACHIANS.**

By G. A. BOULENGER, F.R.S.

(Plate 5, figs. 3-6.)

1. *OREOPHRYNELLA QUELCHII*, Blgr. (Plate 5, fig. 3.)

This tiny toad was described by me as the type of a new genus in 1895 (Ann. & Mag. N. H. [6] xvi. pp. 125 & 522) from specimens collected on the summit of Mt. Roraima by Messrs. Quelch and McConnell. Numerous specimens have since been obtained at the same altitude (8500-8600 feet).

I have now the pleasure of describing a second species of the same genus, from the base of the mountain.

2. *OREOPHRYNELLA MACCONNELLI*, sp. n. (Plate 5, fig. 4.)

Closely allied to *O. Quelchii*, but distinguished by the more prominent snout, projecting much beyond the mouth, and by the greater distal expansion of the digits, which end in distinct truncated disks. Interorbital space broader than the upper eyelid. First toe much longer than second, as long as fourth; no distinct subarticular or metatarsal tubercles; the first and second toes appear to be opposable to the fourth and fifth, both fascicles being bound by the thick integument, and the third toe, which is the shortest, being free between them. The tarso-metatarsal articulation reaches the eye. Upper parts covered with small, smooth, feebly prominent warts; lower parts with flat granules. Olive-brown above, with lighter marblings, and a series of small yellowish spots, forming a line on each side of the back from the eye to the groin, continued obliquely across the upper surface of the femur; upper lip yellowish, with two dark brown bars below the eye; lower parts whitish.

From snout to vent 22 millim.

A single specimen from the base of Mt. Roraima, 3500 feet.

*OTOPHRYNE*, g. n. *Engystomatidarum*.

Pupil round. Tongue large, oval, truncate and free behind; no teeth on the palate; two denticulated dermal ridges in front of the pharynx. Tympanum very distinct. Fingers free, toes webbed at the base, the tips merely swollen. Outer metatarsals united by the integument. Precoracoid present, weak; sternum cartilaginous. Sacral diapophyses rather strongly dilated\*.

3. *OTOPHRYNE ROBUSTA*, sp. n. (Plate 5, figs. 5, 5 a.)

Habit stout; head rather small. Snout short, pointed, obliquely truncated at the end and projecting beyond the mouth, which is inferior, well within the lines of the canthi rostrales; nostril equally distant from the eye and the end of the snout; eye rather small, little prominent; interorbital space nearly twice as broad as the upper eyelid; tympanum very large, close to the eye and once and a half its diameter. Fingers short,

\* Osteological characters ascertained by means of a sciagraph kindly prepared by Messrs. Gardiner and Green.

swollen at the end, first nearly as long as but not reaching so far as second. Toes very short, depressed, swollen at the end, webbed at the base, the web continued as a fringe along the sides; no distinct subarticular or metatarsal tubercles. The tarso-metatarsal articulation reaches the tympanum; tibia as long as the foot, two-fifths length of head and body. Skin thick, perfectly smooth, shiny on the upper parts; a strong fold from the eye to the insertion of the thigh. Blackish brown above; groin and hinder side of thighs orange, spotted with black; throat and breast dark brown; belly and lower surface of limbs whitish with some brown dots.

From snout to vent 53 millim.

A single specimen from the foot of Mt. Roraima, 3500 feet.

#### 4. *HYLODES MARMORATUS*, sp. n. (Plate 5, fig. 6.)

Tongue circular, entire; vomerine teeth in two very small oblique groups behind the level of the choanæ. Head a little longer than broad; snout rounded, not prominent, as long as the diameter of the orbit, with obtuse canthus rostralis and concave loreal region; nostril much nearer the tip of the snout than the eye; interorbital space nearly as broad as the upper eyelid; tympanum distinct, one-fourth the diameter of the eye. Digits moderately elongate, with well-developed disks, which are as large as the tympanum, and strong subarticular tubercles; first finger shorter than second; toes quite free; a small, oval, inner metatarsal tubercle. The tibio-tarsal articulation reaches between the eye and the nostril; tibia half the length of head and body. Skin smooth above, with feeble oblique glandular ridges on the occiput; belly granular. Grey-brown above, with brown, dark-edged marblings on the head and body and cross-bars on the limbs; dark bars radiating from the eye; grey-brown beneath.

From snout to vent 19 millim.

A single specimen from the foot of Mt. Roraima, 3500 feet.

#### 5. *HYLA ALBOMARGINATA*, Spix.

### EXPLANATION OF PLATE 5.

Fig. 1.	<i>Neusticurus rudis</i> .	Upper view.
1 a.	" "	Lower view.
1 b.	" "	Upper view of head, $\times 2$ .
1 c.	" "	Lower view of head and neck, $\times 2$ .
2.	<i>Prionodactylus leucostictus</i> .	Upper view.
2 a.	" "	Lower view.
2 b.	" "	Upper view of head, $\times 2$ .
2 c.	" "	Lower view of head and neck, $\times 2$ .
3.	<i>Oreophrynella Quelchii</i> .	Upper and lower views.
4.	" <i>Macconnelli</i> .	Upper and lower views.
5.	<i>Otophryne robusta</i> .	Upper view.
5 a.	" "	Open mouth.
6.	<i>Hylodes marmoratus</i> .	Upper view.

## CRUSTACEA.

By Dr. J. G. DE MAN.

(Plate 6.)

PALÆMON (MACROBRACHIUM) QUELCHI, sp. n.

Thirty-seven specimens, only five or six of which are full-grown, were collected in the Upper Mazaruni river at an altitude of 2500 feet, and one young specimen was captured at an altitude of 3500 feet on the Mt. Roraima range. Amongst the former is but one ova-bearing female, the rest are both males and young females, the full-grown specimens being all males.

This pretty species, that I have the pleasure to name after Mr. J. J. Quelch, is apparently closely allied to *Pal. potiuna*, F. Müller, from the Itajahy river, State of Santa Catharina, and to *Pal. Iheringi*, Ortm., from the State of São Paulo, both in the south of Brazil; but it is no doubt different, the second legs presenting characters *intermediate* between those of the two quoted species. *Palæmon Quelchi* is evidently their representative in British Guiana. One full-grown specimen only is still provided with both legs of the second pair, in the others one of them is lost. The ova-bearing female has also lost these legs, and in the numerous young individuals one leg of this pair or even both are often wanting.

*Palæmon Quelchi* belongs to the species of *small* size, the adult individuals measuring only 55 millim. from tip of rostrum to the extremity of the telson. Examined under a rather strong lens the cephalothorax presents a fine and rare punctation, on which one observes a short pubescence, for the rest it appears smooth. The rostrum (Pl. 6. figs. 1-4), vertically moderately deep, is rather short, reaching only the end of the antennular peduncles or even only the middle of their terminal joint, so that it does not extend to the end of the antennal scales. The upper margin, usually very slightly convex above the eyes, gradually descends downwards and carries *seven, eight, or nine* low, rather equidistant teeth, the first *two* of which commonly stand on the cephalothorax, but often only *one* tooth stands on it, the second being placed above the orbital margin. The lower margin is usually armed with *two* teeth, often, however, with *one* only. The formulæ for 34 specimens are the following:—

5 specimens $\frac{9}{2}$ ;	4 specimens $\frac{9}{1}$ ;	9 specimens $\frac{8}{2}$ ;
5     " $\frac{8}{1}$ ;	5     " $\frac{7}{2}$ ;	5     " $\frac{7}{1}$ ;
1 specimen $\frac{6}{2}$ .		

The hepatic spine is small and placed below and posterior to the somewhat larger antennal one. The apex of the telson, as usual shorter than the lateral appendages and the flattened upper surface of which bears the two ordinary pairs of small spinules, is triangular with a quite short median spine; the inner spinules are somewhat longer than the median point and considerably longer than the outer ones.

The free end of the antennal scales is obtusely angulated internally and reaches a little

further forward than the short spine at the extremity of the external margin. The shortest of the three antennular flagella is distinctly serrate and exceeds the free end of the antennal scales by its whole length. The external maxillipedes project with their terminal joint beyond the peduncles of the outer antennæ.

The first pair of legs exceed, in the full-grown male, the antennal scales by two fifth parts of their carpus; the latter is once and two-thirds as long as the hand, the fingers very slightly longer than the palm.

The second legs are considerably stouter and longer than the first and somewhat unequal. In the largest male, which is 54 millim. long, both legs (Pl. 6, figs. 5 & 6) are slightly longer than the body and both exceed the antennal scales by the whole length of the carpus. The cylindrical merus widens slightly towards its distal end. The carpus of both legs appears at first sight just as long as the merus, but measured exactly it appears always *very slightly longer than it*. The carpus, quite narrow at base and here much narrower than the distal end of the preceding joint, regularly widens towards its distal extremity, so that it has a conical shape and its diameter at the distal end is a little broader than that of the merus. *The carpus appears, therefore, two and a half to three times as long as thick at its distal extremity.* The chela is two and a half times as long as the carpus, and in both legs the palm measures almost two-thirds the length of the whole hand. The palm of the larger chela is *distinctly broader* than the widened distal end of the carpus, being a little more than once and a half as broad; the palm is about three times as long as broad, and its width measures almost one-fourth the length of the whole hand. The palmar portion of the hand appears *slightly broader than thick*, the proportion being as 6 : 5; it is everywhere rounded both on the upper and lower surface and on the sides. When the chela is looked at from above, the outer margin of the palm appears straight, but the inner slightly convex, and the inner border of the chela is a little concave at the base of the fingers. The pointed fingers leave, when closed, a narrow interspace between them, in the middle about as broad as the fingers themselves; the latter are almost cylindrical. The immobile finger is nearly straight and tapers but very slightly towards the tip; the dactylus, however, is somewhat curved and tapers more regularly. Each finger is armed with a strong conical tooth; that of the index is placed just in the middle of the finger, that of the dactylus a little beyond it; three much smaller obtuse teeth are observed between each conical tooth and the articulation, and the third of these small teeth is double. On each finger a sharp cutting-edge runs between the conical tooth and the tip.

The smaller chela (fig. 6) bears a close resemblance to the other, but the difference between its width and its height or thickness is still smaller, so that the palm appears almost cylindrical and but slightly broader than the carpus. The fingers are regularly tapering, the dactylus is less curved, and the interspace between both is small, only half as broad in the middle as the fingers. The toothing is about the same, but the dactylus bears six small obtuse teeth between the large conical tooth and the articulation.

In the younger individuals the fingers are comparatively longer, so in a young male, long. 36 mm., the palm is  $4\frac{1}{2}$  mm., the fingers 4 mm. long; the former,  $1\frac{1}{8}$  mm. broad, is three times broader than long and 1 mm. thick.



Fig. 7 represents the second leg of a female, long. 42 mm., devoid of eggs. The merus measures 5 mm., the carpus  $5\frac{1}{2}$ , the hand  $11\frac{1}{2}$  mm., of which the palm occupies 6 mm. The palm is  $1\frac{1}{2}$  mm. broad, the carpus at its distal extremity  $1\frac{1}{2}$  mm. The toothing of the fingers, figured fig. 7a, appears in this young individual still very feeble, the dactylus showing only three teeth, the index also, but these are less prominent, more rounded.

The second legs of these young individuals bear a close resemblance to *Pal. potiuna*, F. Müll. (*vide* Ortmann, 'Os Camarões da agua doce da America do Sul,' S. Paulo, 1897, est. i. fig. 9), but there can be no doubt that this species is a different one, for this resemblance is only exhibited by quite young individuals.

The second legs are on all their joints roughened by small thorny points, that are crowded and numerous on their outer margin, less numerous on the rest of their surface, and those of the lower surface and of the inner margin are distinctly somewhat longer; these legs are glabrous, devoid of hair, except a rare short pubescence, only perceptible under a lens.

The ambulatory legs of the third pair project with a third of their propodites beyond the antennal scales, their carpopodites reaching as far forward as the peduncles of the outer antennæ; the legs of the fifth pair finally extend as far forward as the external maxillipeds, but do not reach the free end of the antennal scales. The ambulatory legs are rather slender. So are the meropodites of the third pair of the largest male 8 mm. long, 1.25 mm. thick, the propodites 7.9 mm. long and 0.84 mm. thick, so that the former are little more than six, the latter nine to ten times as long as broad; for the meropodites of the fifth legs (Pl. 6. fig. 8) these numbers are 7.5 mm. and 1 mm., for the propodites 7.9 mm. and 0.7 mm., so that the meropodites are seven to eight, the propodites eleven times as long as broad. The dactylopodites are short, measuring about one-fourth the length of the propodites. The posterior margin of the propodites bears two rows of spinules, so that in the third legs there are nine or ten spinules in the outer and six or seven in the inner row. The ambulatory legs are a little hairy, but for the rest quite smooth: the hairs are very short and fine, and arranged partly two and two in longitudinal rows; so that one row runs along the posterior margin of the meropodites. The eggs are few in number but large, having a diameter of  $2\frac{1}{2}$  mm. Concerning the single female carrying these eggs, which is 38 mm. long from tip of rostrum to the extremity of the telson, the following may be remarked:—The rostrum (fig. 2) reaches to the middle of the terminal joint of the antennular peduncles; the upper margin that descends obliquely downward bears seven teeth, the second of which is placed above the orbital margin; the lower border is armed with two teeth, the interspaces are as usual ciliated. The external maxillipeds exceed the antennal peduncle only by half their terminal joint. The first legs project only with the hands beyond the free end of the antennal scales; the hands measure just two-thirds the length of the carpus. The legs of the third pair reach to the end of the antennal scales, those of the fifth to the end of the antennal peduncles. The meropodites of the third pair are  $4\frac{1}{2}$  mm. long and  $\frac{3}{4}$  mm. broad; the propodites are 4 mm. long and  $\frac{1}{2}$  mm. broad.

*Palæmon potiuna*, F. Müller, differs at first sight by the chelæ of the second legs

having the fingers as long or even, according to Ortmann's figure, *slightly longer than the palm*. *Palæmon Iheringi*, Ortm. (*l. c.* p. 211, est. i. figs. 7 e, 8) is apparently also different. The carpus of the second legs, indeed, does not gradually and regularly widen towards its distal end, but suddenly, so that the form is different.

*Measurements in millimetres.*

	No. 1.		No. 2.	No. 3.	No. 4.	No. 5.	No. 6.
Length from tip of rostrum to extremity of abdomen .....	54		52	48	47	45	
„ of second legs .....	Left. 58	Right. 61	Left shorter. 46	36	43	32	39
„ of merus .....	10½	10½	8½	6	7½	5½	7
„ of carpus .....	10½	11	9	6½	7½	6	7½
Width of the carpus at the distal end .....	4	4	3½	2½	3	2½	2½
Length of chela .....	25	28½	18½	14½	20½	12½	18
„ of palm .....	15½	18	11	8½	13	7	10
Breadth „ .....	4½	6½	3½	2½	4½	2½	3½
Height „ .....	4	5½	3	2½	3½	2	2½

No. 6 is a detached leg.

EXPLANATION OF PLATE 6.

Figs. 1-4. *Palæmon Quelchi*, sp. n. Anterior portion of carapace in four examples,  $\times 3$ : Fig. 1 of the largest male, long. 54 mm.; Fig. 2 of the ova-bearing female, long. 38 mm.; Fig. 3 of another male, long. 52 mm.; Fig. 4 of a young male, long. 35 mm.

Fig. 5, right, and Fig. 6, left leg of the second pair of the largest male, long. 54 mm.,  $\times 2$ .

Fig. 7. One of the legs of the second pair of a female without eggs, long. 42 mm.,  $\times 2$ ; 7 a, toothing of both fingers of this specimen,  $\times 25$ .

Fig. 8. Fifth leg of the largest male, long. 54 mm.,  $\times 5$ .

*List of the known Species of the Genus Palæmon, Fabr. s. s., May 1900.*

[The species printed in *italics* inhabit America and the West Coast of Africa. The locality indicated as the habitat is in every case taken from the first published description of the species. Of those marked with an asterisk the descriptions were not accessible to me when preparing this list.]

1. *acanthosoma*, sp. n. (?) Nob. Katau, New Guinea.
2. *acanthurus*, Wgm. Coast of Brazil.
3. *acutirostris*, Dana. Sandwich Islands.
4. *africanus*, Bate. Tambo river.—According to von Martens, 1869, = *Gaudichaudii*, M.-E. The Tambo river, mentioned by Spence Bate as the habitat of his species, would, according to von Martens, be situated in Peru! Confer also: Miers, 'On a Collection of Crustacea from South America,' 1877.
5. *africanus*, Kingsl. West Coast of Africa.—Thallwitz, 1891, supposes this species to be identical with *Pal. macrobrachion*, Herkl.

6. *Alphonsianus*, Hfm. Réunion.—This species is identical with *Pal. dispar*, Marts. Confer : de Man, 'Crustacea collected by Max Weber,' 1892, p. 437.
7. *altifrons*, Hend. Delhi ; River Jumna ; Lahore.
8. *amazonicus*, Hell. Amazon river.
9. *americanus*, Bate. Lake of Amatitlan, Guatemala.—According to von Martens, 1869, = *brachydactylus*, Wgm., and according to Miers, 1888, = *jamaicensis*, Hbst.
10. *Appuni*, Marts. Porto Cabello, Venezuela.  
„ var. *equatorialis*, Ortm. Ecuador.
11. *asper*, Stps. In fresh water and in the river near Canton, China.—This species is identical with *nipponensis*, de Haan.
12. *asperulus*, Marts. Shanghai.
13. *Audouini*, Hell. Red Sea.
14. *Audouini*, Bate. Off New Zealand.
15. *australis*, Ortm. = sp., de M., 1887 ? Queensland.—Ortmann, 'Decapoden-Krebse des Strassburger Museums,' p. 708.
16. *aztecus*, Sauss. Gulf of Mexico.
17. *bariensis*, de M. Fresh water, Flores.
18. *boninensis*, Stps. Bonin Islands, in hill-streams.
19. *Borellii*, Nob. San Lorenzo (Jujuy) ; San Luis.
20. *brachydactylus*, Wgm. East coast of Mexico.
21. *brasiliensis*, Hell. Camaroes, Brazil, fresh water.—According to Ortmann a locality of this name does not exist in Brazil. Camaroes would be the Spanish name of these prawns ! ('Decapoden-Krebse des Strassburger Museums,' p. 711.)
22. *brevicarpus*, de Haan. Japan.—Confer : de Man, in Max Weber's 'Crustacea,' 1892, p. 418.
23. *brevimanus*, Fabr. India.
24. *cementarius*, Poepp. Mouth of the River Aconcagua.—This species is identical with *Bithynis longimana*, Phil. Confer : 'Zoologischer Anzeiger,' 1894, p. 266 ; von Martens, 'Ueber einige ostasiatische Süßwasserthiere,' 1868, p. 65 ; and Miers, l. c. 1877, p. 662. According to Miers it is a variety of *Pal. Gaudichaudii*, M.-E.
25. *callirrhoe*, de M. Mandai river, Ketoengan river (Borneo).
26. *carcinus*, Fabr. India †.
27. *consobrinus*, Sauss. Gulf of Mexico, off Vera Cruz.
28. *coromandelianus*, Fabr. India.
29. *Danæ*, Hell. Sydney.
30. *Dayanus*, Hend. Orissa, Calcutta, Lahore.
31. *dasydactylus*, Streets. Tide-water of the Coatzacoalcas river, Isthmus of Tehuantepec.—According to Ortmann (l. c.) = *mexicanus*, Sauss.
32. *Desausuri*, Hell. New Granada.
33. *dispar*, Marts. Isle of Adenare.
34. *dolichodactylus*, Hilgd. Mozambique.
35. *dulcis*, n. sp. ?, Thallw. North Celebes.
36. *elegans*, de M. Sinagar, Buitenzorg, Java.
37. *endeensis*, de M. - Flores.
38. *ensiculus*, S. Sm. Pará.
39. *equidens*, Dana. In the sea near Singapore.
40. *esulentus*, Thallw. - North Celebes.

† Fabricius indicates the rivers of America as the habitat of this species—of course, wrongly.

41. *euryrhynchus*, Ortm., = *latimanus*, Marts. Fiji Islands.—Confer: de Man, in Max Weber's 'Crustacea,' 1892, p. 482.
42. *faustinus*, Sausa. Antilles.
43. *fluvialis*, Streets. Coatzacoalcos river, among the Cordilleras.
44. *forceps*, M.-E. Rio de Janeiro.—According to von Martens, 1869, = *acanthurus*, Wgm.
45. *formosensis*, Bate. River Tamsuy, Formosa.
46. *gangeticum*, Bate. Patna, India.
47. *Gaudichaudii*, M.-E. Chili.—Confer: von Martens, 'Ueber einige oostasiatische Süßwasserthiere,' 1868, p. 65.
48. *gracilimanus*, Rand. Sandwich Islands.
- \*49. *gracilirostris*, Miers. Upolu, Samoa Islands.
50. *grandimanus*, Rand. Sandwich Islands.—Confer: von Martens, *l. c.* 1868, p. 45.
51. *heterochirus*, Wgm. East coast of Mexico.
52. *Hildebrandti*, Hilgd. Madagascar.
53. *Hilgendorfi*, Cout. East coast of Madagascar, region of large forests.
- \*54. *hirtimanus*, Oliv.
- \*55. *hispidus*, Oliv.—According to Heller, 'Synopsis der im rothen Meere vorkommenden Crustaceen,' 1861, this species occurs in the Red Sea.
56. *Horstii*, de M. Celebes, fresh water.
57. *Idæ*, Hell. Borneo.
- ,, var. *idella*, Hilgd. Pond near Matomondo, Ungúu; Usaramo (German East Africa).
- ,, var. *mammillodactylus*, nov. var.?, Thallw. North Celebes, Luzon.
- ,, var. *subinermis*, Nob. St. Joseph river, Innawi (British New Guinea).
58. *Iheringi*, Ortm. State of São Paulo, Brazil (fresh water).
59. *jamaicensis*, Hbst. Rivers of Jamaica.
60. *japonicus*, de Haan. Japan.
61. *javanicus*, Hell. Java.
62. *Jelskii*, Miers. Guiana (Oyapok).
63. *Lamarrei*, M.-E. Coast of Bengal.
64. *laminatus*, Gollm., = *jamaicensis*, juv.? Caracas.—Confer: von Martens, *l. c.* 1869, p. 24.
65. *lampropus*, de M. Celebes, Timor (fresh water).
66. *lanceifrons*, Dana. Luzon.
67. *lar*, Fabr. India.
68. *latidactylus*, Thallw. North Celebes.
69. *latimanus*, Marts. Philippines (Isle of Samar).
70. *lepidactyloides*, de M. Flores (fresh water).—Confer: de Man, in 'Notes from the Leyden Museum,' vol. xv. p. 308.—According to Coutière = *lepidactylus*, Hilgd.
71. *lepidactylus*, Hilgd. Mozambique (Quellimane, Tette).
72. *longidigitum*, Bate. Habitat unknown.
73. *longimanus*, Fabr. East India.
74. *longimanus*, Hffm., = *ornatus*, Oliv. Réunion.—Confer: de Man, in 'Notes from the Leyden Museum,' vol. i. p. 172.
- \*75. *longimanus*, Phil., = *cementarius*, Poepp. Chili (La Ligua river).—Confer: Philippi, in 'Zoologischer Anzeiger,' 1894, p. 266.
76. *longipes*, de Haan. Japan.
77. *macrobachion*, Herkl. West Coast of Africa (Boutry, near Dixcove).
78. *madagascariensis*, Hffm. Nossy-Faly.
- \*79. *Malcolmsonii*, M.-E. Nagpore.—Confer: Henderson, 'A Contribution to Indian Carcinology,' 1893, p. 444.

80. *Malliardi*, Rehts. Mauritius (Creole river, Black river).
81. *Mariæ*, Cout. River Ivaloina, near Tamatave (Madagascar).
82. *mayottensis*, Hffm. Mayotte, Nossy-Faly.—Confer: de Man, in 'Notes from the Leyden Museum,' vol. i. 1879, p. 173, where it is proved to be a local variety of *ornatus*, Oliv.
83. *mexicanus*, Sausa. Coast of Mexico.
84. *modestus*, de M. Flores, fresh water.
85. *Montezumæ*, Sausa. Gulf of Mexico, off Vera Cruz.
86. *Moorei*, Calman. Lake Tanganyika.
87. *mossambicus*, Hilgd. Mozambique (Quellimane).—According to Coutière = *dispar*, Marta.
88. *multidens*, Cout. River Kotofotsy, arm of the Onilahy, Madagascar.
89. *Nattereri*, Hell. Brazil (Rio Negro).
- \*90. *niloticus*, Roux. Nile.—Confer: von Martens, *l. c.* 1868, p. 66.
91. *nipponensis*, de Haan. Japan.
- \*92. *ohionis*, S. Sm. Ohio, Mississippi.
93. *Olfersii*, Wgm. Coast of Brazil.—Confer: Greeff, in 'Sitzungsber. Gesells. z. Beförderung der gesammten Naturw. zu Marburg,' 1882, p. 30.
- \*94. *ornatus*, Oliv., = *lar*, Fabr.
95. *parvus*, Hffm. Nossy-Faly.
96. *Patsa*, Cout. River Mahanara (east coast of Madagascar); arm of the River Onilahy (west coast of the same island).
97. *paucidens*, Hilgd. Togo Country.
98. *Petersii*, Hilgd. Mozambique (Tette).
99. *pilimanus*, de M. Sumatra.  
     ,, var. *leptodaactylus*, de M. Java (Buitenzorg).
100. *placidulus*, de M. Saleyer, Celebes, Flores, Timor, fresh water.—Confer: de Man, in 'Notes from the Leyden Museum,' vol. xv.
101. *placidus*, de M. Sumatra.
102. *potiporanga*, F. Müll. Itajahy river.
103. *potiuna*, F. Müll. Itajahy river.
104. *punctatus*, Rand., = *jamaicensis*, Hbat. East Indies?—Confer: Kingsley, in 'Bull. Essex Institute,' vol. xiv. 1883, and Miers, in E. Whymper, Supplementary Appendix to 'Travels amongst the Great Andes of the Equator,' 1888.
105. *Quelchi*, de M. Upper Mazaruni river, Mount Roraima (British Guiana).
106. *reunionnensis*, Hffm. Réunion.—Confer: de Man, in Max Weber's 'Crustacea,' 1892, p. 454.
107. *Ritsemæ*, de M. Atjeh.
108. *Rosenbergii*, de M. Andai, New Guinea.
109. *ruber*, Hess., = *ornatus*, Oliv. Fiji Islands.—Confer: Ortmann, 'Decapoden-Krebse des Strassburger Museums,' p. 705.
110. *rudis*, Hell. Ceylon.
111. *Savignyi*, Bate. Bermuda Islands.
112. *scabriculus*, Hell. Ceylon.
113. *sexdentatus*, Streets. Tide-water of the Coatzacoalcos river, Isthmus of Tehuantepec.—According to Ortmann ('Decapoden-Krebse des Strassburger Museums,' p. 711) this species is identical with *mexicanus*, Sausa.
114. *sinensis*, Hell., = *nipponensis*, de Haan. Shanghai.—Confer: de Man, in 'Notes from the Leyden Museum,' vol. i.
115. *singalagensis*, Nob. Aier Mantecior, near Mount Singalang (Sumatra).
116. *sintangensis*, de M. Sintang, Borneo.



117. *spectabilis*, Hell., = lar, Fabr. Tabiti.—Confer: de Man, in Max Weber's 'Crustacea,' p. 445.
118. *spinimanus*, M.-E. Antilles and coast of Brazil.—According to von Martens, *l. c.* 1869, = *Olfersii*, Wgm.
119. sp., de Man, in Zool. Jahrbücher, ii. 1887. Sydney.
120. sp., de Man, in Archiv für Naturg. 1888, p. 557. Amboina.
121. sp. (*Macrobrachium* ?), de Man, in Max Weber's 'Crustacea,' 1892, p. 488. Celebes, fresh water.
122. sp., Miers, in Ann. & Mag. Nat. Hist. ser. 5, v. p. 384 (1880). Java.
123. sp., Thallwitz, 'Decapoden-Studien,' 1891, p. 19. North Celebes.
124. *sundaicus*, Hell. Java.  
     —, var. *bataviana*, de M. Batavia.  
     —, var. *brachydactyla*, Nob. Amboina.  
     —, var. *de Mani*, Nob. Amboina.—According to Nobili the last-named variety is identical with that described by de Man in Zoolog. Jahrbücher, ix. Abth. f. System. p. 783, fig. 72.
125. *superbus*, Hell. Shanghai.
126. *tenellus*, S. Sm. Polvon, Occidental Department of Nicaragua.
127. *tranquebaricus*, Fabr. East India.
128. *Trompii*, de M. Ketoengau river, Mandai river, Siutang (Borneo).
129. *ustulatus*, Nob. Rigo, British New Guinea.
130. *vagus*, Hell., = lar, Fabr. Amboina.—Confer: de Man, in 'Notes from the Leyden Museum,' vol. i.
131. *Vollenhovenii*, Herkl. Coast of Guinea.—Confer: de Man, in 'Notes from the Leyden Museum,' vol. i. 1879.
132. *Weberi*, de M. Celebes, fresh water.

## MYRIOPODA AND ARACHNIDA.

By R. I. POCKOCK.

Class *DIPLOPODA*. (MILLIPEDES.)

Family POLYDESMIDÆ.

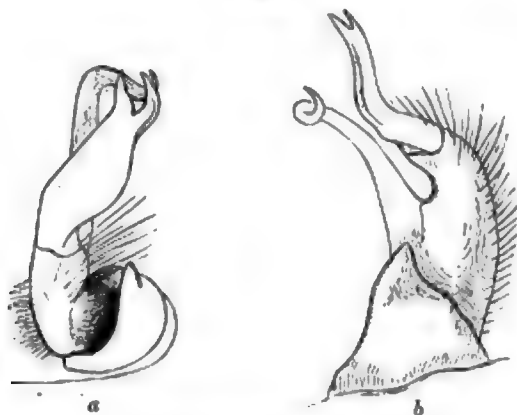
Genus ODONTOPELTIS, Pocock.

ODONTOPELTIS MACCONNELLI, sp. n.

♂. *Colour* black or very dark blackish brown, with the external half of the keel bright or dull red or yellowish brown, and, at least on the anterior terga, a median transverse yellowish or red patch along the posterior border; caudal process not pale; antennæ blackish; legs blackish brown or deep reddish brown, sterna brownish yellow. *Dorsal integument* smooth and shining or finely coriaceous; *keels* horizontal, with smooth edges, the posterior margin transverse and in the same straight line as the posterior border of the tergum, as far back as the eleventh or twelfth somite; the posterior angle not spinate, mostly acutely angled, rarely approaching a right angle; the anterior angle widely rounded and obtuse. *Caudal process* triangular, narrowly truncate posteriorly.

*Anal sternite* triangularly pointed; sternum of eighteenth somite wider behind than the length of the coxæ of the last pair of legs. Copulatory limbs as in fig. 1, the basal segment armed externally with a large downwardly-directed conical process; second segment furnished with numerous thickly-set short hairs on the inner side at the base and externally with many long bristles; giving off distally two long processes, an upper and a lower, directed obliquely forwards and downwards; the upper process runs forwards

Fig. 1.

*Odontopeltis Macconnelli*, sp. n.

a. Lower view of left copulatory leg. b. Lateral view of external surface of right copulatory leg.

and downwards with a slight curve, then turns sharply externally, and ends in a sharp tip curving upwards and forwards; the inferior process is laminate, but narrower at base and distally than in middle, with a slight sigmoid flexure when seen from the side; seen from below its inner edge is directed straight forwards in its basal third, then obliquely forwards and outwards, the outer edge being convex; distally the process ends in two sharp prongs—an inner straighter and an outer semicircularly curved forwards.

♀. Stouter than male, with smaller keels.

♂. Total length 43 mm.; width 6.

♀. „ 43 „ ; „ 7.

*Loc.* Summit of Roraima, 8600 feet alt.

#### Genus EURYURUS, C. Koch.

##### EURYURUS ATRATUS, sp. n.

♀. *Colour*: dorsal area a uniform black, ventral area a little paler. *Head* with a smooth, oval, pale-coloured prominence in the middle line just between and below the antennæ; a curved row of six setal pores above the labrum. *Dorsal area* smooth and polished. *Keel* of second somite laterally emarginate, leaving the anterior and posterior angle acute and subdentate; lateral margin of keel of third and fourth somites with a notch behind the anterior angle, which is thus subdentate; remaining keels with posterior margin finely serrulate, concave; angle acute and becoming more and more acute and produced in the posterior region of the body; lateral margin of keels even, slightly

subsinate in front of the pores; anterior angle convexly rounded and on the anterior somites slightly prominent. *Caudal process* narrowly oval posteriorly. *Anal sternite* distinctly bituberculate.

Total length 41 mm.; width 6·7.

*Loc.* Base of Mount Roraima (3500 feet).

Resembling in colour *E. fumigatus*, Peters, from Bogota (MB. Ak. Berlin, 1864, p. 624), but differing from Colombian specimens in the British Museum that I have referred to *fumigatus* in having the lateral border of the keels of the second tergite emarginate, the keels larger, and the caudal process narrower towards the extremity.

### Class ARACHNIDA.

#### Order ARANEÆ. (SPIDERS.)

#### Family BARYCHELIDÆ.

#### Genus CYRTOGRAMMOMMA, Poc.

#### CYRTOGRAMMOMMA MONTICOLA, Poc.

*Cyrtogramomma monticola*, Poc. Ann. & Mag. Nat. Hist. (6) xvi. pp. 139-140 (1895).

*Loc.* Summit of Mt. Roraima (8600 feet).

This genus and species were based upon a single female specimen. Additional examples containing adults of both sexes enable me to supplement the original

Fig. 2.



a. Extremity of palpus of male of *Cyrtogramomma monticola*. b. Eyes of ditto. c. Vulva of *Anyphana Quelchii*. d. Tibial spur of palpus of same. e. Tibial spur of palpus of *Trechalea Macconnelli*.

description by stating the characters of the male and some additional features of the female.

♂. *Colour*, as in ♀, a deep blackish brown; hairs mostly olive-black, those on the carapace, especially laterally, shining golden red, extremities of protarsi on upperside also paler. *Carapace* flatter than in ♀, its length equal to patella + three-fourths of the tibia of the first and fourth leg, barely equal to protarsus of fourth. *Labium* (in ♂ and ♀) armed with a row of cusps varying in number from about four to nine; maxillæ also internally cuspidate. *Palpus* in ♂ with the tibia almost as in ♀, but armed on the inner side with six or more long strong spines, those at the distal end protecting the palpal organ when lying at rest backwards beneath the tibia; tarsus long, like that of the ♀, but scopulate only in its distal half beneath, excavated posteriorly; spine of palpal organ nearly straight, long, almost as broad at the base as the bulb and tapering away to a fine point. Tibia of first leg without apical spur; tibia of all the legs armed with many long and strong spines: protarsus of first leg armed with two inferior spines at base of scopula, which covers less than the apical half of the segment; protarsus of second armed with three spines, scopula short and scanty as in first leg; protarsi of third and fourth armed with many long and strong spines. (In the ♀ the anterior legs and palpi are armed only with spiniform setæ and the scopulæ extend practically to the base of the protarsi.)

*Measurements in millimetres*.—♂. Total length 12; length of carapace 6.5, of 1st leg 23, of 4th leg 26.

#### Family ANYPHÆNIDÆ.

##### Genus ANYPHÆNA, Sund.

##### ANYPHÆNA QUELCHII (Poc.).

*Aysa Quelchii*, Pocock, Ann. & Mag. Nat. Hist. (6) xvi. pp. 140-142, fig. (1895).

*Loc.* Roraima (summit, 8600 feet). Adult males and females.

On his previous expedition to Roraima, Mr. Quelch procured the only two specimens of this species, an adult male and an immature female. I take the opportunity of figuring the vulva (fig. 2 c) of the adult female and the tibial spur of palpus of the male (fig. 2 d).

#### Family PISAURIDÆ.

##### Genus TRECHALEA, Thorell.

(= *Triclaria*, C. Koch.)

##### TRECHALEA MACCONNELLI, sp. n.

*Colour*. Carapace blackish, with pale lateral border and narrow radiating pale stripes. the intervals between the radiating lines also ornamented with short flavous lines. Clypeus pallid, with a broad dark band on each side, running upwards and inwards from the lateral angle; mandible black, clothed with long yellow hairs, the yellow field

interrupted by dark lines. Legs and palpi blackish banded with pale; femora with about four flavous patches, sometimes fusing together or connected with flavous stripes; patella distally flavous; tibia with median and apical flavous stripe; protarsus with broad but indistinct distal flavous stripe; femora reddish below at the base; sternum and coxæ olive-yellow; upperside of abdomen covered with greyish hairs intermixed with black bristles; black behind, with two bright yellow patches above the spinners; lower side orange-yellow.

Palp with tibial spur as in fig. 2 *e*.

*Measurements in millimetres*.—Total length 16, carapace 8.5; 1st leg 64, 4th leg 73; tibia of 1st leg 17, of 4th 17.

*Loc.* Mount Roraima (base, 3500 feet).

This species may be readily recognized by the form of the tibial spur of the palp.

### Family ARGIOPIDÆ.

#### Genus ACROSOMA, Perty.

##### ACROSOMA SCHRIEBERSII, Perty.

*Acrosoma Schriebersii*, Perty, Delect. Anim. Artic. p. 194, tab. 38. fig. 9 (1830-34).

*Loc.* Base of Roraima, 3500 feet.

#### Genus ARANEUS, Linn.

##### ARANEUS AUDAX, Blackwall.

*Epeira audax*, Blackwall, Ann. Mag. Nat. Hist. (3) xi. p. 29 (1863).

*Loc.* Upper Mazaruni River.

### Order SCORPIONES.

#### Family CHACTIDÆ.

#### Genus BROTEOCHACTAS, Poc.

*Broteochactas* and *Hadrurochactas*, Pocock, Ann. Mag. Nat. Hist. (6) xii. pp. 77-78 (1893); id. Journ. Linn. Soc., Zool. xxiv. p. 399 (1893); Kraepelin, MT. Mus. Hamb. xi. pp. 175, 178; id. Das Tierr., Scorp. etc. p. 172 (1899).

Four species referable to this genus have hitherto been discovered, namely:—

1. *BROTEOCHACTAS GOLLMEI*, Karsch, Mitth. Münch. ent. Ver. 1879, p. 133 (*Chactas*): *nitidus*, Pocock, Journ. Linn. Soc., Zool. xxiv. p. 399, pl. xxix. figs. 7, 7 a (1893) (*Broteochactas*).  
*Loc.* Trinidad and Venezuela.
2. *BROTEOCHACTAS DELICATUS*, Karsch, Mitth. Münch. ent. Ver. 1879, p. 134, ♀: *opacus*, Karsch, op. cit. p. 134, ♂ (*Chactas*); *panamensis*, Thorell, Bull. Soc. Ent. Ital. xxv. p. 27 (1894) (*Broteus*).

*Loc.* British Guiana, Colombia, Panama.

3. *BROTEOCHACTAS SCLATERI*, Pocock, Ann. Mag. Nat. Hist. (6) xii. p. 80 (1893) (*Hadrurochactas*): ? *Schaumii*, Karsch, Z. Naturw. liii. p. 406 (1880); ? *quinquedentatus*, id. op. cit. p. 405 (*Chactas*).

*Loc.* British Guiana (*W. L. Sclater*).

[Kraepelin (MT. Mus. Hamb. xi. p. 178, 1894, and Das Tierr., Scorp. etc. p. 173, 1899) states that *B. Sclateri* is identical with *B. Schaumii* of Karsch, and possibly with *quinquedentatus* of this latter author, both of which were recorded, though no doubt erroneously, from India. But the presence of only five pectinal teeth in the latter forbids, to my mind, such an opinion. *B. Schaumii*, judging from Kraepelin's description, is closely allied to *B. Sclateri*, but the fact that the third caudal segment is higher than wide in *Schaumii*, and wider than high in the two known examples of *Sclateri*, makes the synonymy doubtful.]

4. *BROTEOCHACTAS PARVULUS*, Pocock, Ann. Mag. Nat. Hist. (6) xix. p. 364 (1897); Kraepelin, Das Tierr., Scorp. etc. p. 174 (1899).

*Loc.* Amazonas, Santarem (*F. O. P. Cambridge*).

The following well-marked new species were discovered by Messrs. McConnell and Quelch:—

*BROTEOCHACTAS GRANOSUS*, sp. n.

*Colour.* Carapace, terga, and tail almost black; legs, palpi, and vesicle of tail deep reddish brown, the legs with paler line and spots; fingers black. *Carapace* and *terga* entirely covered with fine close-set granulation; ocular tubercle coarsely punctured; carapace a little longer than the first and second caudal segments, a little shorter than the fifth. *Coxæ* and *sterna* finely punctured, the last sternite weakly and closely granular laterally. *Tail* more than four times the length of the carapace, narrowed posteriorly, the segments nearly parallel-sided: the first wider than long; second slightly longer than wide; fourth not twice as long as wide; fifth a little more than twice as long as wide; intercarinal spaces finely granular; inferior and infero-lateral keels obsolete on segments 1 and 2, scarcely traceable on segment 3, represented on segment 4 by irregularly arranged larger granules; superior and supero-lateral keels weak, weakly granular; inferior surface of fifth coarsely granular between the keels; vesicle granular, narrower than third segment, wider than high.

*Chelæ* finely granular; upperside of humerus and brachium with coarser granules between the keels; upperside of hand covered with a reticulation of fine granules; inner surface similarly granular; back of hand coriaceous; fingers granular at base. Width of hand equal to length of external keel of hand-back, less than length of movable digit; digits longish, movable as long as the carapace, immovable about twice as long as its basal width. Femora and tibiæ of *legs* granular, the granules intermixed with punctures on the tibia, following segments closely punctured; tarsi short, not twice as long as high, convex above, incrassate distally, armed with long setæ arranged more or less regularly in two rows.

*Measurements in millimetres.*—Total length 46; length of carapace 6·5, of tail 29·5; width of 1st segment 3·5, of 5th 2·8; width of hand 5·5; length of hand-back 5, of movable finger 8·5.

*Loc.* Base of Mt. Roraima (3500 feet alt.).



*BROTEOCHACTAS POROSUS*, sp. n.

*Colour.* Trunk and tail blackish brown; fourth and fifth segments of tail and vesicle paler, reddish; legs also reddish brown, chelæ with humerus and fingers blackish, hand and brachium redder.

*Carapace*, except on the normally smooth tracts, very distinctly punctured, especially the area around and between the eyes, with very fine close-set granulation on its lateral slope. *Terga* similarly punctured, with a few very fine granules in front and on the sides, the granules and punctures scarcely distinguishable with a hand-lens; the tergum of seventh abdominal somite much more distinctly granular, with larger granules along the lateral border and two series forming indistinct crests on each side. *Sterna* punctured, the fourth and fifth more closely than the others, the third with a distinct smooth patch in the middle of its posterior half.

*Tail* barely four times as long as the carapace; carapace as long as first, second, and half the third segments, and about as long as the fifth; scarcely narrowed posteriorly; all the segments wide, the second nearly twice as wide as long, the fourth about as wide as long; fifth one-third longer than wide, abruptly narrowed behind; segments punctured throughout; the superior, supero-lateral, and infero-lateral keels strong and granular; the inferior median crests almost obsolete on segment 1, more evident on segments 2 and 3, but represented by irregularly arranged granules; on segment 4 the granules assume a more definite, but still incomplete arrangement in two parallel rows; median lateral keel present on segment 1, represented by a few granules on segments 2 and 3, absent on segment 4; fifth segment with its upper edges granular and sharp, a distinct median lateral keel in the anterior half of the side, and three distinct and granular inferior keels, the area between them also serially granular. *Vesicle* narrower than the tail, wider than high, punctured but not granular below.

*Chelæ* punctured even to the tips of the fingers; humerus with upper keels granular; brachium with upper anterior keel obsoletely granular; hand wide, distinctly though not strongly carinate, not granular, except slightly so on the inner surface; width of hand about equal to length of hand-back; fingers long and slender, in contact, the movable as long as the carapace, nearly twice the length of the hand-back.

*Legs* punctured, not granular; tarsi furnished beneath with long, close-set, irregularly arranged bristles; the fourth tarsus long, lightly convex above, about three times as long as high.

Pectinal teeth 10 (♂ ♀); the teeth longer in ♂.

*Measurements in millimetres.*—Total length 24; length of carapace 3.5, tail 15.

*Loc.* Summit of Mt. Roraima (8600 feet).

Some of the distinguishing features of these two species of *Broteochoactas* are set forth in the following table:—

- a. Infero-lateral crests on all the caudal segments strong, as strong as the supero-lateral; inferior medians present and granular; the integument punctured throughout; terga in male mostly weakly granular; vesicle smooth; hand with two finger-keels, smooth, more globular; fingers long and slender, movable as long as carapace. (Of small size, 25 mm. in length.) . . . . . *porosus*, sp. n.

- b.* Infero-lateral crests on anterior three caudal segments obsolete; inferior medians absent; dorsal integument not noticeably punctured; terga closely granular throughout in male; vesicle granular; hand granular, less globular, with compressed inner edge, without finger-keels.
- a'*. Carapace ( $\delta$ ) entirely covered with close-set granules; sterna minutely and closely punctured throughout; lower surface of tail finely and closely granular and punctured; legs also densely and closely punctured; fingers longer, the movable as long as carapace, immovable more than twice as long as its basal width. (Of large size, 46 mm. in length.) . . . . . *granosus*, sp. n.
- b'*. At least the upper portion of the carapace smooth; sterna and lower surface of anterior segments of tail smooth and polished, not punctured or granular; legs mostly smooth and polished; femora at most weakly granular; fingers shorter, movable shorter than carapace, immovable not twice as long as its basal width.
- a''*. Tail very thick, width of first caudal segment considerably exceeding the width of the hand, and equal to length of first and second caudal segments taken together; hand very smooth, rounder, its inner edge less compressed, with keel of underhand obsolete; tarsi longer, more thickly covered below with long hair . . . . . *Sclateri*, mihi.
- b''*. Tail much thinner, width of first segment generally much less than, rarely equal, to width of hand, and less than sum of length of first and second caudal segments; hand at least with its inner edge granular and subcompressed; tarsi shorter and more scantily clothed with shorter hairs . . . *Gollmeri*, *delicatus*, *parvulus*.

(For tabulation of the characters of the last three species, see my paper in Ann. Mag. Nat. Hist. (6) xix. pp. 365-366, 1897; and Kraepelin, Das Tierr., Scorp. etc. p. 173, 1899.)

## HYMENOPTERA, HEMIPTERA HETEROPTERA, HOMOPTERA, NEUROPTERA, AND ORTHOPTERA.

By W. F. KIRBY, F.L.S., F.E.S.

(Plate 6. figs. A, B.)

THE few specimens of these Orders which have been submitted to me for identification consist almost exclusively of common and well-known South American species. A few species, mostly immature, are hardly in a condition to be determined with certainty. These are one Forficulide, three Blattidæ, and one Pentatomide. One Hemipteron I have described as new.

The two species noted from the greatest elevation (*Polistes annularis* and *Sympetrum gilvum*) are southern representatives of forms found in North America.

## HYMENOPTERA ACULEATA.

## APIDÆ.

## MELIPONA INTERRUPTA

*Melipona interrupta*, Latr., Humb. & Bonpl. Voy. i. p. 291, pl. 20. fig. 3 (1811).

*Melipona fasciculata*, Smith, Cat. Hym. Ins. Brit. Mus. ii. p. 406, n. 25 (1854).

Roraima, 3500 feet.

## VESPIDÆ.

## POLISTES ANNULARIS.

*Vespa annularis*, Johansson, Amœn. Acad. vi. p. 413. n. 93 (1763).

Roraima, 8600 feet.

## MUTILLIDÆ.

## MUTILLA LARVATA.

*Mutilla larvata*, Klug, Nova Acta Acad. Leop. x. p. 310, pl. 22. fig. 6 (1821).

Roraima, 3500 feet.

## MUTILLA QUADRUM.

*Mutilla quadrum*, Klug, Nova Acta Acad. Leop. x. p. 320, pl. 23. fig. 8 (1821).

Roraima, 3500 feet.

## FORMICIDÆ.

## DOLICHODERUS BISPINOSUS.

*Myrmica bispinosa*, Oliv. Enc. Méth. vi. p. 502. no. 60 (1791).

Roraima, 3500 feet.

A considerable number of specimens.

## HEMIPTERA HETEROPTERA.

## COREIDÆ.

## ACANTHOCEPHALA SURATA.

*Diactor suratus*, Burm. Handb. Ent. ii. (1) p. 334. n. 2 (1835).

Roraima, 3500 feet.

## REDUVIIDÆ.

ACROCORIS PERARMATA, sp. n. (Pl. 6. fig. A ; B, profile of head.)

Long. corp. 27 millim.

*Male*. Rufo-testaceous, clothed with a fine grey pile, all the spines tipped with reddish. Head long, the part behind the eyes slightly longer than that before ; two long pointed spines near together just behind the antennæ ; antennæ with the first joint very long,

blackish, with two whitish bands near each extremity, second joint about  $\frac{1}{2}$  as long as the first, whitish, with the extremity blackish; third joint about as long as first, blackish towards the base, and yellowish beyond, blackish again at its junction with the fourth joint, which is yellowish and about as long as the second. Front lobe of thorax with two strong erect spines at the back; middle lobe with four, two in the middle, and two lateral, all at about equal distances apart. Clavus brown. First joint of rostrum yellowish, the remainder deep black, the tip extending just beyond the base of the head. Legs unarmed, thickly pubescent, more or less blackish on the outer side; tarsi black. Abdominal segments with four small lateral spines on the basal half, and three long, triangular, whitish, lateral spots on each side beyond the middle. Scutellum with a very slight terminal spine, if any.

Roraima, 3500 feet.

This curious insect does not seem to have much resemblance to any described species

## HEMIPTERA HOMOPTERA.

### FULGORIDÆ.

#### ACRÉPHIA PERSPICILLATA.

*Cicada perspicillata*, Fabr. Spec. Ins. ii. p. 322. n. 1 (1781).

Roraima, 3500 feet.

## NEUROPTERA ODONATA.

### LIBELLULIDÆ.

#### SYMPETRUM GILVUM.

*Diplax illotum*, var. *gilva*, De Selys, Ann. Soc. Ent. Belg. xxviii. p. 43 (1884).

Roraima, 8600 feet.

## ORTHOPTERA.

### LOCUSTIDÆ.

#### CHROMACRIS SPECIOSA.

*Gryllus speciosus*, Thunb. Mém. Pétersb. ix. p. 40, pl. 14. fig. 1 (1824).

Roraima, 3500 feet.

## EXPLANATION OF PLATE 6.

Fig. A. *Acrocoris perarmata*, sp. n.

Fig. B. " " profile of head.

**COLEOPTERA.**

By C. O. WATERHOUSE, V.P.E.S.

**CARABIDÆ.****OXYCREPIS LEUCOCERA**, Lacord.

A single example.

**DYTISCIDÆ.****RHANTUS ELEGANS**, Waterh.

Several specimens found at an elevation of 8600 feet. A single example only was obtained on a former occasion.

**LUCANIDÆ.****CHARAGMOPHORUS LINEATUS**, Waterh.

This genus and species were described from a single male example. Other males and two females have now been found at 8600 feet.

The female has the elytra as in the male, with lines of very small grey scales; but the head and thorax are shining. The mandibles are short. The head is sparsely punctured posteriorly, rather strongly transversely impressed in front and strongly and closely punctured. The thorax is rather more convex than in the male, a little narrowed anteriorly, obtusely angular at the sides at a short distance from the base, moderately finely punctured, the punctures rather unequal, not very sharply defined, separated from each other by two to three diameters of a puncture; the margins are impressed; the disk is longitudinally impressed. The front tibiæ have the five teeth rather stronger and more approximate than in the male; the posterior tibiæ have a small acute tooth at the middle.

**DASCILLIDÆ.****EXAGONTUS**, gen. nov.

Mentum a little broader than long, slightly narrowed anteriorly, corneous; ligula broad and transverse, acuminate at the sides; labial palpi three-jointed, the basal joint elongate, the second a little shorter, pear-shaped, the third somewhat the same shape but inverted, acuminate at the apex. Maxillæ with two delicate subequal lobes; the galea consists of two portions, the basal part parallel, the apical portion shorter, clothed with stiff hair; the lacinia terminates in a curved acute tooth, which is surrounded by curved stiff bristles. Maxillary palpi rather long, robust, hairy; the basal joint rather short, narrowed at its base; the second joint stouter, at least twice as long as broad, gradually and not very much narrowed towards the base; the third joint similar in shape but a little shorter; the fourth a little longer than the second, club-shaped, acuminate at the apex. Mandibles strong, curved, concave below, very acute at the apex, with a small

tooth about the middle. Labrum rather large, subquadrate, rounded in front. Head convex, deflexed, but in no way covered by the pronotum, parallel behind the eyes, narrowed in front. Eyes rather prominent, coarsely faceted. Antennæ placed a little in front of the eyes, widely separated at their base, eleven-jointed, of moderate length, of nearly equal thickness throughout, except the slender third joint; composed of cylindrical joints, clothed with stiff pubescence; the second joint globose, the third joint very narrow at the base, the following joints gradually narrower towards their bases. Thorax strongly transverse, the side with a strong tooth-like prominence about the middle. Scutellum triangular. Elytra broader than the broadest part of the thorax, one-third broader than long, flattened dorsally; the surface uneven, irregularly punctured.

Prosternum much reduced, with a diamond-shaped process between the coxæ, the coxal cavity completely open posteriorly.

Mesosternum slightly inclined, with a slight, sharply margined concavity in which the prosternal process rests.

Metasternum rather short; the episterna broad, a little narrowed posteriorly. Abdomen composed of five visible segments below. Anterior coxæ strongly transverse; intermediate coxæ globose; posterior coxæ very narrow externally, very wide internally.

Tibial spurs small but distinct. Tarsi five-jointed; the basal joint nearly as long as the two following taken together; the fourth the broadest, concave above, so that it has a tendency to be bilobed, clothed with soft pubescence below; fifth joint not very long, with divaricating claws.

I have some doubt as to the affinities of this genus. The structure of the antennæ points to affinity with the Ptinidæ, near *Hedobia*; but the broader, flatter form, the freely exposed head, the transverse anterior coxæ, and internally dilated posterior coxæ would place it in the Dascillidæ, where I now propose to place it. No doubt the Ptinidæ and Dascillidæ should be placed nearer together than is usual in collections.

#### EXAGONTUS DENTICOLLIS, sp. n.

Elongato-oblongus, parum convexus, fusco-castaneus, sat nitidus, brevissime griseo-pubescent; capite nigrescente, crebre punctato; thorace utrinque dente valido instructo; elytris crebre punctatis, pube gisea variegatis, impressionibus nonnullis notatis.

Long.  $3\frac{1}{2}$ , lat. 2 mill.

The antennæ are moderately robust, the third joint more slender, the fourth to tenth joints a little longer and broad, cylindrical, united to each other by their centres; the eleventh joint a little longer, elongate-oval. Apical joint of the maxillary palpi black. The elytra are brown, closely punctured, with numerous lines of greyish-yellow pubescence giving a mottled appearance. Each elytron has a large transverse impression below the scutellum, another about the middle, one below the shoulder; the surface of the apical portion is uneven, and in certain positions three slight interrupted costæ may be traced.



## TENEBRIONIDÆ.

## CYRTOSOMA MONTANUM, sp. n.

Oblongum, nitidum; capite, thorace femoribusque fere nigris; elytris æneis, tenuiter striatis; ore, antennis, tibiis tarsisque piceo-flavis.

Long. 11, lat.  $5\frac{3}{4}$  mill.

Head finely and rather closely punctured. Antennæ with the six terminal joints gradually wider. Thorax finely but distinctly and rather closely punctured, with a very slight, transverse impression above the anterior angles and above the posterior angles; the sides with two obtuse not very prominent angles. Scutellum pitchy. Elytra rather wider than the thorax, one-quarter longer than broad, rather straight at the sides, obliquely narrowed at the apex, finely striated, the striæ indistinctly punctured, the interstices scarcely convex on the back, but at the apex and at the sides they are slightly angularly raised in the middle; the fourth and fifth striæ unite posteriorly about one-third from the apex, the third and fifth unite nearer the apex, and the second and sixth within the apical angle. The underside of the insect is for the most part pitchy red, shaded with black on the metasternum and abdomen.

## LAMIIDÆ.

## ALCIDION SEXNOTATUM, sp. n.

Elongatum, angustum, fuscum, pube grisea vestitum; thorace basi constricto; elytris fasciis punctisque numerosis fuscis ornatis, singulo elytro ad apicem oblique truncato, angulo saturali obtuso, angulo externo rectangulare; antennis gracilibus, corpore multo longioribus. ♂.

Long. 11, lat. 4 mill.

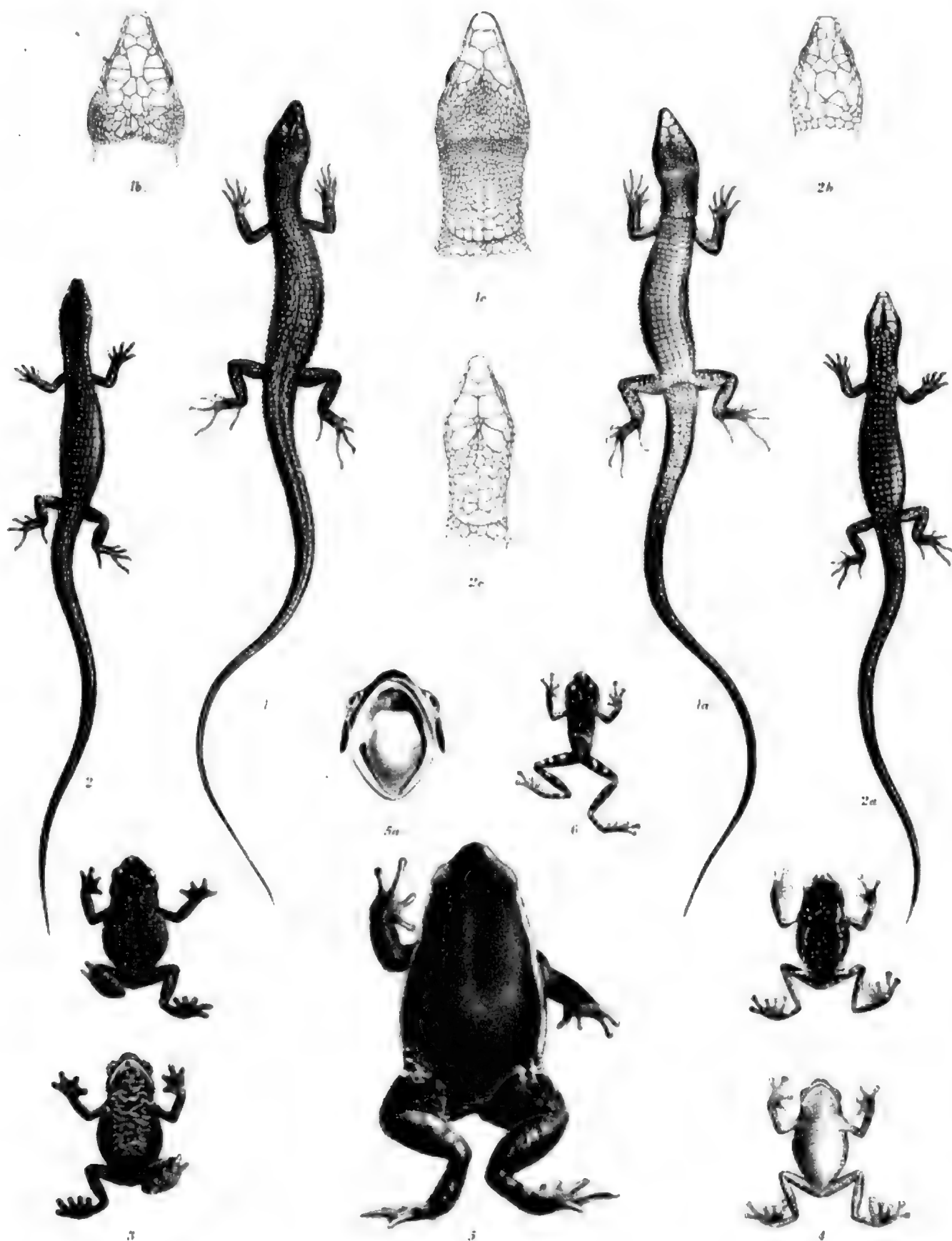
Compared with the majority of the species of this genus, this is very elongate and narrow. The antennæ are very long; the basal joint is much narrowed at the base, then quite straight and parallel to the apex; the joints are tipped with black and have some black pubescence, which forms a slight tuft at the apex of the third joint. The thorax is short and transverse, lightly impressed on the disk, arcuately narrowed anteriorly, slightly constricted at the base; the middle of the disk and three or four small spots at the sides are brown. The elytra have scarcely any trace of costæ; the basal crest is well marked but not acute; the basal area is brown, with two vague oblique vittæ of ashy pubescence marked with brown punctures; at the middle there is an irregular ashy fascia (descending at the suture) marked with brown punctures; behind this is a fascia formed by five elongate spots placed side by side, the sutural one lower down than the others; in the apical area there are six brown spots, three of which are placed so as to make **VI** on the left elytron.

The following species, not of very special interest, were found at an elevation of 3500 feet:—

*Passalus transversus*, Dalm.; *Antichira dichroa*, Mannerheim; *Pelidnota lævissima*, Burm.; *Pyrophorus noctiluca*, Linn.; *Strongylium hæmorrhoidalis*, Fabr.; *Heilipus carinirostris*, Schönh.; *Cratosomus subangulatus*, Schönh.; *Sphenophorus hemipterus*, Linn.; *Trachyderes interruptus*, Dup.; and *Jamesia globifera*, Fabr.





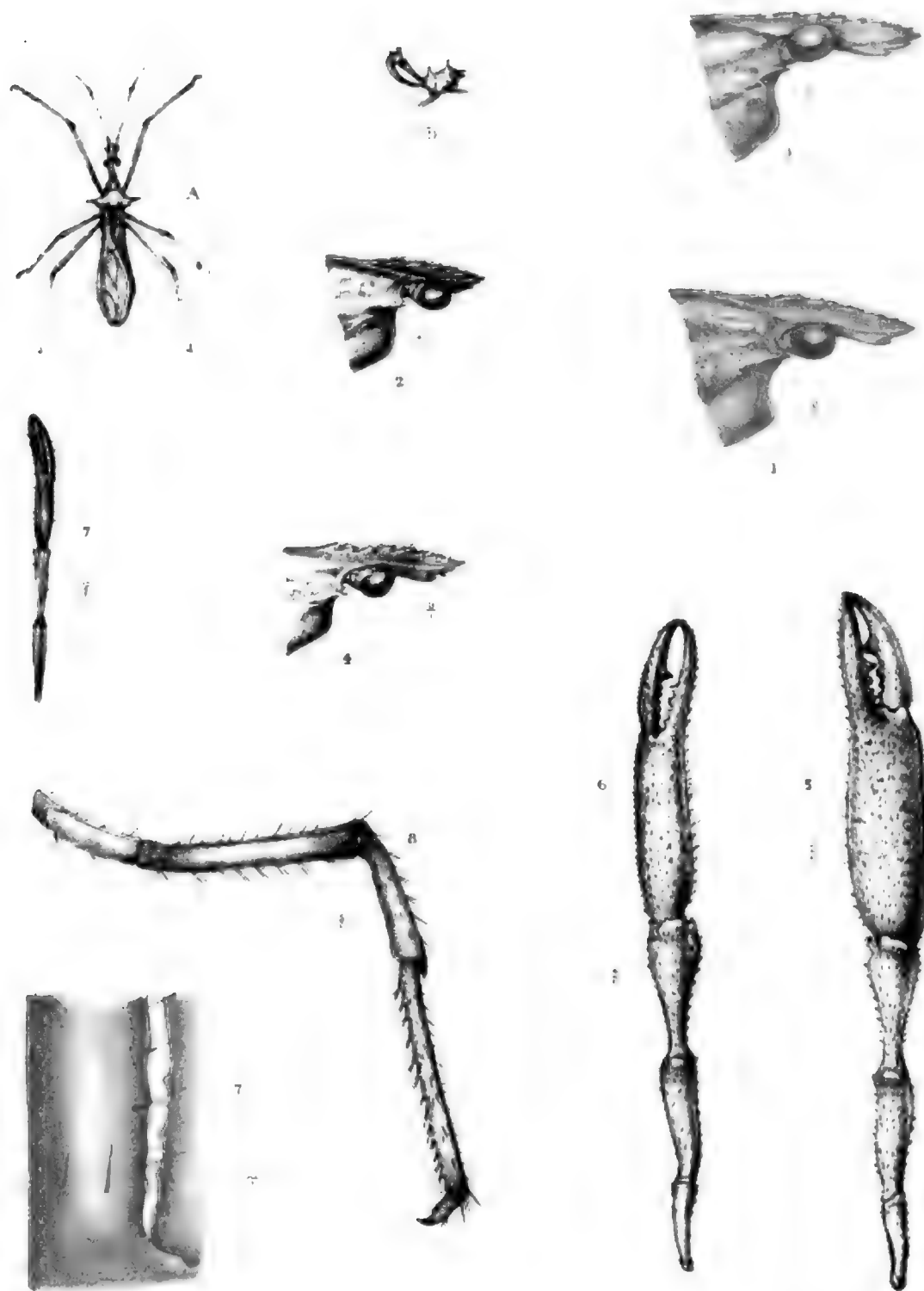


FIGURES OF THE LATERAL

MINIATURE BROS. 1891

1. *NEUSTICURUS RUDES*. 2. *PHYLLODACTYLUS LEUCOGASTRUS*.  
3. *PHYLLODACTYLUS MACCONNELLII*. 4. *PHYLLODACTYLUS RUPESTRIS*.

5. *PHYLLODACTYLUS MACCONNELLII*. 6. *PHYLLODACTYLUS RUPESTRIS*.  
7. *PHYLLODACTYLUS MACCONNELLII*. 8. *PHYLLODACTYLUS RUPESTRIS*.



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CRUSTACEA AND INSECTA FROM R. RAIMA

### III. *On the Structure and Affinities of Echiurus uncinatus.*

By ALICE L. EMBLETON, B.Sc. (Communicated by Prof. G. B. HOWES, Sec. L.S.)

(Plates 7-10.)

Read 7th June, 1900.

THE observations recorded in this paper were made by me in the Zoological Laboratory of the Royal College of Science, London, during January, February, and March 1900, under the direction of Professor Howes and Mr. M. F. Woodward, to both of whom I owe a debt of gratitude for their generous help and advice.

The material was obtained by Professor Howes from Professor Mitsukuri, of Tokyo, through the kindness of Mr. H. Lyster Jameson, who had intended to report upon it in his recently published paper in the Naples 'Mittheilungen,' but for want of time had been prevented from so doing.

The specimens, numbering between 90 and 100, were in alcohol, and had been preserved in corrosive sublimate. On the whole they were in very good condition, though much contracted, resulting in great variability of shape both as regards the entire body and the different organs; in several individuals, parts of the alimentary canal were forced out through bursts in the body-wall, presumably caused by sudden and violent contraction. To a large extent these *post-mortem* changes obscured many observations which, on fresh or uncontracted material, could have been made with greater ease and certainty.

Doubtless this is the species mentioned—though not named specifically—by Willemoes-Suhm\* as occurring on the Japanese coast, where apparently it lives in great abundance, for he says: "Ein Echiurid der den Fischern als Köder dient und wohl in Schlamm dicht am Ufer vorkommt. Der 3-4 Zoll lange Wurm stimmt ganz mit den Merkmalen der Gattung *Echiurus* überein, hat aber hinten nicht zwei Hakenkränze, sondern nur einen."

The average length of the body is about 7 or 8 cm.: all the specimens are narrowest at the posterior end, widening out gradually, as a veritable sac, between this and the proboscis. The term "proboscis" is used, though that organ is, in all, represented merely by a bluntly-pointed præ-oral lobe of triangular outline (Pl. 7. figs. 1-2, *pb.*); it cannot be doubted, however, that this is due to its state of contraction, for in cutting a series of microscopic sections of the anterior end of the body there was nothing to suggest that the proboscis was missing, as is so often the case with the British form, *Echiurus Pallasii* (Guérin), called "*E. vulgaris*" by Forbes, Forbes & Goodsir, Sars, O. Schmidt, and Metzger.

\* "Von der Challenger Expedition, Briefe von R. v. Willemoes-Suhm an C. Th. v. Siebold, vii.," Zeitschr. wiss. Zool. Band xxvii 1876, p. cii.



The only previous description of this species is that given by Drasche \*, who had but two specimens to work on, with the result that his observations are superficial and limited to three pages. Of his specimens he records: "Beide Exemplaren fehlte der Kopflappen (Rüssel)." It may be that, having so little material, he was misled by the highly retracted state of this organ, which, possessing as it does a very powerful musculature, is very liable to extreme contraction. Even allowing for the contracted condition, this proboscis is a much shorter organ than in *Echiurus Pallasii* or *Thalassema neptuni*, and never assumes the almost ribbon-like form it presents in the latter species.

At the base of the proboscis-lobe is the mouth, placed ventrally (Pl. 7. figs. 1, 2, *m.*).

The whole outer surface of the body is densely papillated (Pl. 1. figs. 1, 2, 4), agreeing in this respect with other species of *Echiurus*: the papillæ show no very definite arrangement, though they tend to run in transverse rows round the body, in which direction also the individual papillæ are elongated (Pl. 7. fig. 4).

As in allied forms, anteriorly on the ventral surface are two recurved setæ (Pl. 7. fig. 1, *s.a.*), pointing outwards and backwards; posteriorly are the characteristic peri-anal hooks (fig. 1, *s.p.*), which in this species form but a single circlet. Drasche gives this as one of the three distinguishing features of the species—hence its name "*unicinctus*" or "one girdle." In speaking of this circlet of setæ, however, he says it is made up of 11 setæ; but on examining my material the number seems to be by no means constant, varying indifferently from 10 to 13 (Pl. 7. figs. 1, 5). The space between the two setæ situated most ventrally is always greater than that between any other two, giving it the appearance of an incomplete ring—though Drasche has observed that the ring is complete ventrally.

Just behind the two anterior hooks, on the ventral side, it is possible to see with a hand-lens two pairs of minute pores among the papillæ; these are the external apertures of the segmental organs or nephridia. The reproductive products are passed to the exterior through these pores.

Referring to the papillæ, Drasche says: "Nur an einer Stelle etwa 5 mm. hinter den Bauchborsten, findet sich ein 5½ mm. breiter Gürtel von 13 Papillenkränzen. Diese Papillen sind etwas grösser als die übrigen und haben die Form von auf die schmale Seite gestellten Ziegeln."

So far as my specimens are concerned no such tract is discernible, though on submitting the body-wall to microscopic examination it is found that in the region of the segmental organs the ordinary unicellular glands occur along with immense compound glands (which will be more fully dealt with below). This particularly glandular belt may correspond to the 13 rows of large papillæ mentioned by Drasche (Pl. 7. figs. 6, 7, *g.*).

Probably the animal secretes a substance with which it lines the tubes or burrows in which it lives, using the two recurved anterior setæ in climbing and its posterior circlet

\* "Ueber eine neue *Echiurus*-Art aus Japan," Verhandlungen des zoologisch-botanischen Vereins in Wien, Band xxx. 1880.

to hold itself in its tunnel. The setæ have a significantly abundant supply of powerful muscles (fig. 12), and the wall of the posterior end of the body is much thicker than elsewhere, on account of the comparatively disproportionate development of the layer of longitudinal muscles (Pl. 7. fig. 9).

*Setæ.*—These agree on the whole with Spengel's description of those in *Echiurus Pallasii*. There is, however, some slight difference observable between the setæ of the anterior pair (Pl. 7. fig. 3) and of the posterior circle; the former are large and very markedly recurved, while the latter are smaller and finer, with but a slight curvature. The anterior setæ project into the body-cavity very conspicuously, and possess numerous strong radiating muscles (Pl. 7. figs. 5, 12; Pl. 10. fig. 40). In minute structure each seta presents a pointed, somewhat flattened free end; about a third of its length back there is a circular constriction, after which the seta widens out again to its blunt extremity, which lies embedded in muscle and a protoplasmic mass from which it originated, and in which young setæ can be seen. The chitin of which the hook is composed exhibits a transverse striation or annulation, less marked at the pointed end. Greeff says there is a fine canal in the substance of the seta at the free end running a short way back; this does not appear to be a canal but to be due to striation, as is so often seen in the ordinary setæ of Chætopoda.

*Body-wall.*—The body-wall varies in thickness in different regions, being thinnest where the body is widest, and thickest at the tapering posterior extremity. It is not unlikely that this is in part caused by differences in the state of contraction, but this alone could not account for the very striking divergence in the proportionate depths of the respective muscle-sheaths (*cf.* Pl. 7. figs. 6, 8, 9, 10).

Microscopic sections of the body-wall serve to show that, in general histological structure, it is almost identical with that of *Echiurus Pallasii* as described by Greeff and Spengel. The epidermis is covered by a well-defined cuticle, which is typical of the whole group; in microscopic preparations this appears as a sharp dark line running along the outer border of the section, pierced by the skin-glands; and beneath this clearly marked band, and abutting on the epidermal cells, a vacuolated layer presents itself, similar to that figured by Jameson\* in *Thalassema neptuni* (Pl. 7. figs. 6, 7, 8, 9, 10).

The epidermis is composed of a single layer of columnar cells, but it is difficult to distinguish them as such, for they are much distorted by the pressure of the numerous unicellular glands and clear cells; the epidermal cells give the appearance of a clear matrix in which these darkly staining bodies seem to be embedded. The nuclei of the epidermal and gland-cells lie at their inner ends, and, as they stain almost as strikingly as the glandular secretion, they form a dark border in section (Pl. 7. figs. 6, 7, 8, 9, 10).

Occasionally the unicellular glands assume giant proportions, become filled with secretion, and might well be mistaken for compound glands (Pl. 7. fig. 6, *g.u.*). In the depressions between the papillæ there are neither gland- nor "trigger-cells"; these latter are seen scattered among the glandular tissue, being most noticeable on the proboscis (Pl. 7. fig. 11).

\* "Contributions to the Anatomy and Histology of *Thalassema neptuni*, Gaertner," Zool. Jahrb. Bd. xii, 1899.

Though on the whole, as is seen, the structure of the body-wall in this Japanese species is largely identical with the descriptions given for allied types, yet in one important point this *Echiurus* differs from others in the group, for it possesses not only unicellular glands but also large compound glands. These occur in immense numbers but are strictly local in their distribution, being restricted to a wide belt in the anterior half of the animal, coincident with the position of the segmental organs. They are very conspicuous, being the most significant structures in sections of the body-wall, whether they be taken in a transverse or longitudinal direction. As Pl. 7. figs. 6, 7 (*g.*) show, these glands are flask-shaped bodies, built up by radially grouped gland-cells (*g.c.*) with delicate walls; the secretion (*s.*) from each component cell is poured into the main duct, which is lined by the cuticle. The nuclei (*nc.*) of the gland-cells collect at the basal ends, and, being large, they make a sharp outline of the flask-like character of the whole organ (Pl. 7. figs. 6, 7). These glands are large and sink far down into the cutis (or connective-tissue strata) (*t.c.*), occasionally coming into contact with the outer circular muscle-sheath (*m.c.*). Invariably the ducts of these glands discharge on the summit of a papilla; and, seeing they are found in no other portion of the skin except near the segmental organs, it is not improbable that their secretion has some function to perform in connection with the ripe eggs, which pass out by the segmental organs. Or, again, the secretion may be used to form a lining to the burrows and tunnels in which the creatures pass their lives. This can only be decided by carefully watching living specimens. Sections of the body-wall of *E. Pallasii*, specimens of which came from St. Andrews, showed however, in the region of the segmental organs, where the compound glands are located in *E. uncinatus*, only unicellular glands. They were similar to those in other parts of the body, being much modified, as Spengel noted, and having each a long tapering neck, attached to an expanded body embedded in the cutis; on the proboscis they were larger than elsewhere, but in no region were there any compound glands such as occur in this Japanese species.

The cutis is beneath the epidermis; it consists of connective-tissue branching cells, with nuclei scattered irregularly throughout. As in all the other layers of the body-wall, no blood-capillaries can be detected (Pl. 7. figs. 6, 7, 8, 9, 10, *t.c.*).

The muscle-sheath comes next; the outermost layer is made up of circularly arranged fibres; below this is a band of longitudinal muscles, followed on the inner side by another layer of circular muscles, showing, however, a slight obliquity as compared with the outer circular layer (*m.c.*).

Sections cut in different parts of the body show all these parts in very varying proportion. Median sections exhibit but feeble papillation, and the unicellular glands are more scattered, while the large compound glands are absent altogether; the cutis and muscle are also proportionately reduced (Pl. 7. fig. 8). A great difference is observable in sections taken through the thickened wall of the posterior end (figs. 9, 10), the immense increase in depth being mainly due to a development of longitudinal muscles; the papillæ are striking, but possess no compound glands.

It is difficult to discover how far the epidermis of the body-wall extends at the posterior extremity of this worm, for there is no definite line of demarcation showing

where the epithelium lining the alimentary canal takes the place of the body integument. A peculiar tissue is present within the anal sphincter, continuing forward some distance beyond the openings of the anal vesicles: it is suggestive of being the glandular epidermis, modified as a result of its morphologically internal position. Its probable significance and relations will be considered more fully in connection with the anal vesicles.

In sections of the body-wall, and more particularly in the region of the proboscis, there are present in the epidermis groups of sensory cells, similar to those figured by Jameson in his paper on *Thalassema neptuni*. Each cell possesses a projecting process or hair, which, piercing the cuticle, forms a trigger-like organ (Pl. 7. fig. 11, *c.s.*); I was unable to trace any connection between these cells and nerve-branches from the lateral trunks in the proboscis. The occurrence of such structures as these sensory cells would appear to be exceptional from what Spengel says in the account he gives of his investigations on *Echiurus Pallasii*: "Beim *Echiurus* habe ich weder bewegliche Cilien noch Starre Haare zu Erkennen vermocht." The only organs of a sensory nature which he finds are those to which he applies the term "becherförmige Sinnesorgane," comparable with those mentioned by Eisig\* as occurring in the *Capitelliden*. In *Sipunculus Andreæ*† found between the gland-cells occasional "Nervendorgane," particularly on the proboscis, but also irregularly distributed over the body. Eisig concludes that what Andreæ calls "Seitenorgane" are in reality the same thing as his "Becherorgane."

*Alimentary Canal.*—The alimentary canal is relatively very long, about 60 cm.; it forms many coils, which are arranged for the most part quite irregularly; yet I find that some of the individual loops are constant in occurrence and disposition. In all cases the mouth leads into a straight buccal cavity, which is fixed to the body-wall by radial and dorsal mesenteric strands. Histologically this tract shows a ciliated glandular epithelium which is thrown into folds, continuous with those on the prostomium. At first the outer layer of longitudinal muscle is very inconspicuous (Pl. 8. figs. 13, 13*a*), but it gradually becomes more pronounced (Pl. 8. figs. 14, 14*a*, *m.l.*). Beyond the region of radial mesenteries the tube becomes narrower and takes an uninterrupted backward course for about an inch; in *Echiurus Pallasii* and *Thalassema neptuni* this region is thrown into a double loop. As before, its lining is glandular, but the walls have become much more muscular; at this point there is always a little knot of 4 to 5 close coils (Pl. 7. fig. 5, *cr.*), in which the muscular elements are greatly reduced and the glandular nature of the epithelium is intensified, the foldings at the same time becoming deeper. From the nature of this coiled portion I judge it to be distensible, so it may function as a crop (Pl. 8. fig. 15). Beyond it, the alimentary canal decreases still more in calibre, and runs almost straight to the posterior end of the body-cavity; its walls are immensely thick, owing to the remarkable development of circular muscle,

\* H. Eisig: "Die Seitenorgane und becherförmigen Organe der Capitelliden," Mittheilungen aus der Zoolog. Station zu Neapel, Bd. i. p. 278.

† J. Andreæ: "Beiträge zur Anatomie u. Histologie des *Sipunculus nudus*, L.," in Zeitsch. wiss. Zool. Bd. xxxvi. pp. 201-258, tabb. 12 u. 13 (1881).

while the longitudinal fibres are almost wanting; the epithelium is correspondingly reduced and is devoid of glands (Pl. 8. fig. 16). This narrow, muscular, non-glandular part is probably to be looked upon as a gizzard, following as it does immediately upon the crop-like region. Jameson describes the "crop" in *Thalassema neptuni* as coming *behind* the gizzard; though it is difficult to see what its use could be in such a position, for the crop is essentially a glandular distensible part in which food collects *before* it can enter the narrow muscular gizzard, where it is crushed previous to its passage into the delicate intestine. I find the cilia in some specimens extend back as far as the beginning of the intestine, though this is apparently an individual variation.

At the posterior end of the body this narrow gizzard, which extends for nearly 5 cm., widens out into the thin-walled intestine, and at the same time it turns forwards, becoming a veritable tangle of complicated coils and loops; mesenteric strands reappear at this point which attach the coils, irregularly, to the body-wall. The beginning of the intestine proper is marked by the appearance of the ciliated groove on the ventral side, which 2.5 cm. further on gives place to the collateral intestine (or siphon), at a point about 12.5 cm. from the mouth. The intestine continues as far as the rectum (or large intestine); its walls are very delicate, possessing very few fibrous elements; its epithelium is glandular and is raised into long slender villi (Pl. 8. figs. 17, 17*a*); above the ciliated groove and collateral intestine runs a band of longitudinal muscle (Pl. 8. figs. 17, 21*a*, 21*b*, *m.l.*), which is continued on the rectum (Pl. 8. fig. 18, *m.l.*). In all the specimens I examined, the origin and end of the collateral intestine are clear and unmistakable, though Drasche says he was unable to find the openings. At its origin (fig. 19), the transition from the ciliated groove to the accessory intestine is very abrupt, the latter standing up from the alimentary canal with a somewhat dilated and swollen end. Posteriorly it passes over gradually into the ciliated groove, ending without a dilatation, about 10 cm. from the anus (fig. 20). On opening the alimentary canal at these points, and pinning back the walls so as to expose the interior, the aperture leading from the collateral intestine into the alimentary canal is plainly visible under a dissecting microscope (Pl. 8. fig. 21, *c.*). Beneath the collateral intestine there is a shallow groove which Jameson has called the "secondary ciliated groove" (fig. 21). The collateral intestine has received various names: it is sometimes referred to as the siphon, or accessory intestine; Spengel calls it the "Nebendarm," while Greeff mistook it for a blood-vessel and speaks of it as the "Darmvene."

The rectum (Pl. 7. fig. 5; Pl. 10. fig. 39, *r.*) is a straight, wide, thick-walled tube, proceeding from the anus along the left side of the nerve-cord as far as the segmental organs; it is held in place by a row of mesenteric filaments inserted exactly opposite the longitudinal muscle, *i.e.* inserted on the dorsal side. At its anterior limit, where it passes into the intestine, there is a marked constriction, though no sphincter muscle can be seen on microscopic investigation. There are two endoparasites in this rectal tract—a probably new species of the Infusorian *Trichodina*, and a Copepod, which is evidently an entirely unknown form\*.

\* This was confirmed by Dr. G. S. Brady, F.R.S., to whom some specimens were submitted.



On comparing the alimentary canal of allied animals, as described by various authors, with this species, I find the part anterior to the intestine has been divided up into numerous distinct regions. Rietsch calls it simply "intestin buccal," but Spengel says it comprises a pharynx, œsophagus, and crop. Jameson finds the œsophagus of *Echiurus* equals the œsophagus and gizzard of *Thalassema*. Greeff does not mention the crop, but in other respects his description agrees with that of Spengel. In this Japanese form I can divide the alimentary canal only into those areas mentioned already, *i. e.* :—

- i. The buccal sac (or pharynx), on the first portion of which are the radial mesenteries.
- ii. The coiled part (or crop).
- iii. The narrow straight part (or gizzard).
- iv. The intestine, bearing the oilated groove and collateral intestine.
- v. The rectum or large intestine, fixed to the left side of the nerve-cord and ending at the anus.

Figs. 13–18, Plate 8, are diagrammatic representations of transverse sections through these various regions, showing the comparative development of the muscular layers and glandular epithelium.

*Blood-Vascular System.*—All the species of the genus *Echiurus* hitherto investigated possess a very characteristic blood-vascular system. *E. Pallasii*, according to Greeff, has two main vessels—a dorsal and a ventral—and "beide Gefässe verlängern sich bis in den Rüssel, das Rückenfass einfach und in der Rückenwandung des Rüssels des Rüsselarterie der mittleren Längsrichtung folgend das Bauchgefäss in zwei Aesten, die in den Seitenrändern unter Entsendung zahlreicher verlaufen." In the proboscis he finds an open communication between the blood system and the body-cavity; anteriorly the dorsal vessel swells out as a contractile heart, while the ventral vessel runs to the hinder end of the body, bound to the ventral surface of the alimentary canal, as the "Darmvene."

Spengel, in working on the same species, gives a very similar account of its vascular system, though he denies the existence of a communication between the vessels and the body-cavity, and does not give any support to the statement that a pulsatile heart is present dorsally. The vessel which Greeff refers to as the "Darmvene" is, as Spengel shows, the "Nebendarm," or collateral intestine. *E. Pallasii*, then, according to Spengel and Rietsch\*, has a ventral vessel running the whole length of the body above the nerve-cord, connected anteriorly by a loop with a short vessel on the dorsal surface of the pharynx and œsophagus: these vessels are found in the proboscis. Jameson gives a similar arrangement for *Thalassema neptuni*; and Shipley† says: "A closed vascular system exists in Echiurids, consisting of a contractile dorsal vessel running along the dorsal surface of the anterior end of the alimentary canal, and continued along the axis of the proboscis. At the tip of the proboscis it bifurcates and each branch descends along the edge until it reaches the base, where, having encircled the œsophagus, the two unite, and are continued as the ventral vessel which runs along the dorsal surface of the nerve-cord, and eventually ends blindly. There is also a vessel which passes from

\* M. Rietsch: "Étude sur les Géphyriens armés ou Echiuriens," in *Rec. Zool. Suisse*, vol. iii. 1886.

† Shipley: *Gephyrea and Phoronis*. The Cambridge Natural History, vol. ii. p. 456.



the ventral vessel and encircles the intestine, opening into the posterior end of the dorsal vessel. In *Echiurus* this same vessel encircles a stout muscle which runs from the base of one of the ventral bristles to the other."

On examining *Echiurus uncinatus*, however, no trace of a closed system of blood-vessels could be found. Many individuals were very carefully opened, but always with the same negative result, there being no dorsal nor ventral vessel with their connecting loop or "muscle-ring" (Pl. 7. figs. 5, 12). Microscopic preparations served but to verify this observation; no vessel exists in relation to the nerve-cord, as is seen in sections of the entire worm and in those of the nerve-cord alone (Pl. 9. figs. 22, 23, 24, 25). If the loop connecting the dorsal and ventral vessels were present, encircling as it does in other species the muscle running between the basal ends of the two anterior hooks, it would appear in the section of the entire worm in that region (Pl. 9. fig. 22, *m.b.*), drawn with the "camera lucida." In similar sections taken through specimens of *Echiurus Pallasii* and *Thalassema neptuni* the blood-vessels were unmistakably present, cut across at various angles. Fearing my methods might be at fault, I applied them to preserved material of *Echiurus Pallasii* and *Thalassema neptuni*; both in dissections and microscopic preparations the vessels occur as Spengel and Jameson describe, being quite clear and distinct. In sections of the proboscis in these two allied forms, the median and lateral vessels are seen at once; but sections in this region of *Echiurus uncinatus* are very different: there are no definite vessels present, but irregular sinuses, which appear to be in two series—conceivably an efferent and an afferent system. The ventral sinuses are elongated transversely (Pl. 9. fig. 26, *s.v.*), and are rather undefined, with thin walls which are scarcely discernible. The upper sinuses, elongated in the opposite direction, are less irregular, with more definite walls (fig. 26, *s.d.*). In tracing the series of sections with great care from the anterior extremity of the proboscis to its union with the body, it is seen that gradually the sinuses widen out, forming large cavities (Pl. 9. fig. 24), which eventually run together in the mouth-region and then merge into the body-cavity. Ova and cœlomic corpuscles are found in all these sinuses (*o.c.*), even at the tip of the proboscis. This is conclusive evidence, establishing the fact that these sinuses are but forward extensions of the cœlom.

These sinuses are in all probability largely connected with the protrusion of the proboscis, functioning much the same way as the blood-sinuses in the foot of the *Lamellibranchia*, where the muscular foot is protruded by an injection of blood into its substance.

Drasche, in speaking of this species, says: "Trotz sorgfältiger Untersuchung beider Exemplare gelang es mir leider nicht, die Gefässschlinge aufzufinden."

The fact that Drasche failed to detect the vascular loop in his two specimens supports my observations, which have the advantage of having been made on many individuals.

*Nervous System.*—The nervous system is arranged in a manner essentially characteristic of all Echiurids. There is a single ventral nerve-cord, extending from mouth to anus (Pl. 7. figs. 5, 12, *n.*); it is fixed to the ventral surface of the body-wall by its lateral branches, which for a short distance are quite free, then they penetrate into the tissue of the body-wall, running parallel with the circular muscles (Pl. 9. fig. 27). These lateral

nerves do not originate accurately opposite one another; they spring from the ventral region of the main cord, and are composed only of nerve-fibres. Spengel found in *Echiurus Pallasii* that these lateral nerves form definite rings or commissures in the body-wall, as nerves from opposite sides meet in the middle dorsal line—their course being, according to him, directly under the rows of papillæ. In *Echiurus unicinctus* the nerve-cord is held in place by its side branches, there being no connective-tissue attachment, such as is found in other forms. Rietsch, in describing the nervous system of *Bonellia minor*, remarks: "Le système nerveux se compose du cordon ventral dépourvu de renflements ganglionnaires, et fixé aux téguments par un mésentère." Though it does not agree with this form of attachment, yet it is not seated directly on the body-wall as in *Thalassema neptuni*, of which Rietsch observes: "Ce tronc nerveux n'est pas, comme chez la *Bonellie*, relié aux téguments par un mésentère; il repose directement sur la musculature." The cord is, in *Echiurus unicinctus*, free from the body-wall, except in so far as its fine lateral branches fix it in position, by becoming embedded in the musculature.

Owing to the contraction of the body-wall, the central nerve-cord in these preserved specimens is thrown into wavy folds (Pl. 7. figs. 5, 12; Pl. 9. fig. 27, *n.*); this condition makes it easy to see that the cord is free of the body-wall but for the attachment of the nerve-branches.

Anteriorly the cord bifurcates (Pl. 7. fig. 12; Pl. 9. figs. 23, 24, 27); the two limbs, passing round the buccal cavity, enter the substance of the proboscis, at the tip of which they meet, thus forming a true circum-œsophageal ring. In forms such as *E. Pallasii*, or *Bonellia*, where the proboscis is a very extensive organ, this nerve-loop is necessarily much elongated. But in the species under consideration, the proboscis being scarcely more than a prostomial lobe, the nerve-ring is almost as compact as in the Earthworm (Pl. 9. fig. 27).

Similarly, at the posterior end the cord splits into equal halves; and these enter into close relation with the wall of the rectum. It is not easy to follow these two branches, but they apparently divide up into finer ramifications which supply the muscles of the anal circle of setæ.

There are no ganglia in the ventral cord.

The outline of the cord in transverse section (Pl. 9. fig. 28) is seen to be rather flattened dorso-ventrally, and is not circular as in *Echiurus Pallasii* (*vide* Greeff, Spengel). The cord has a coating of nerve-cells (*c.*), most marked dorso-laterally—ventrally the cellular elements are fewer and more scattered. These nerve-cells vary much in size; they enclose a central mass, made up of ramifying nerve-fibres (*f.n.*), the majority of which run longitudinally as is seen in longitudinal sections (Pl. 9. fig. 30, *f.n.*). Many of the fibres constituting this central fibrous mass are not nervous, but are inward extensions of the protective connective-tissue sheath which covers the cord. The nuclei which lie scattered throughout this fibrous area may belong to these connective-tissue elements, or to the nerve-fibres, but from the preserved material it is impossible to form a conclusive opinion on this point. In this outer sheath, the longitudinal muscles are much less conspicuous than in similar sections of the nerve-cord of *Echiurus Pallasii*, or of *Lumbricus* (Pl. 9. figs. 31, 32, *sh.*).

Running through the dorsal region of the cord, embedded in the cellular coat, is a structure which Greeff refers to as the "central canal," in spite of its excentric position (Pl. 9. figs. 28, 32, *c.n.*). Spengel calls it the "Neuralkanäle," and says: "Ein Gebilde problematischer Natur nämlich einen Längskanal, der dicht unter der dorsalen Mittellinie verläuft," but how far it runs he is not able to say. Greeff, however, observes of it: "Dieser Kanal aber communicirt mit der Leibeshöhle, ist ein Theil derselben, der zunächst aus dem, wie wir oben gesehen haben, mit dem Blutgefäß-system in directer Verbindung stehenden Kanalsysteme des Rüssels hervorzugehen scheint."

In all my preparations, however, this "canal" has a similar structure and configuration to the so-called "giant fibres" of the Earthworm. I have in Pl. 9. figs. 31, 32, made comparative drawings of the dorsal region of the nerve-cord of *Lumbricus* and of *Echiurus uncinatus*, both preserved and stained in the same way (Ehrlich's hæmatoxylin and eosin or orange gave the most satisfactory results). Though *Lumbricus* has three such structures and *Echiurus* but one, the identity is very striking. The same reagents, used on the nerve-cord of *Echiurus Pallasii*, gave results as in the two former cases. In the Earthworm, however, it was possible to trace the connection between the ganglion-cells and the "giant fibres,"\* being much more difficult to find with the central "fibre" than with the lateral ones. Partly I could trace the connection in *Echiurus uncinatus*, though not in such a way as to render the fact beyond dispute.

*Anal Vesicles.*—Situated at the posterior end of the body-cavity is a pair of very characteristic organs, generally known as the "anal vesicles," though they are occasionally referred to as the "posterior nephridia."

In general form and histological structure, these vesicles show almost complete agreement with those of *Echiurus Pallasii* as described by Spengel. The observations were carried out with difficulty owing to the highly-contracted condition of the vesicles. Drasche evidently met with the same obstacle, for the only mention he makes of these organs is that "in beiden Exemplaren von brauner Farbe, liessen wegen ihres macerirten Zustandes nur schlecht die Wimpertrichter erkennen." However, in my specimens the ciliated funnels are quite recognizable, even in a piece of a contracted vesicle, which was very slightly stained with alum-carmin and then clarified in oil of cloves. Under the microscope this preparation had the appearance of a mass of diverticula, composed of very delicate tissue; the ciliated funnels (Pl. 10. fig. 33, *f.*), which took the stain rather more deeply than the surrounding tissue, were plainly observable among the diverticula (*d.*). Under a higher magnification the component cells could be made out: those forming the diverticula possess very little protoplasmic contents, the nucleus lying apparently in a vacuole (fig. 34, *d. & nu.*); but the cells forming the funnels contain much granular protoplasm (*pp.*) very slightly vacuolated, and nuclei which stain darkly (*c.c. & f.*).

Among the numerous specimens I examined, occasionally there occurred vesicles not wholly contracted; and such a piece of uncontracted material, treated with the same reagents as before, shows the vesicle-wall smooth and unfolded, as in fig. 35. The wall

\* Cf. Friedländer: "Beiträge zur Kenntnis des Centralnervensystems von *Lumbricus*," Zeitschr. f. wiss. Zool. Bd. xlvii. 1888.

is very delicate, consisting of an epithelium of flattened cells (*ep.*), through which run interlacing muscle-fibres (*f.m.*), forming an irregular network. The nuclei of these cells are large and conspicuous, while the cell boundaries are quite distinct, though Spengel says in *Echiurus Pallasii* they are usually indiscernible. He also denies the existence of a special system of blood-vessels which, according to Greeff, run in the vesicle-wall—in my preparations I see nothing to suggest that such a system of canals is present. Greeff also says: “die Innenfläche der Analkiemmen ist mit wimpernden Cilien besetzt”; this is certainly not true of *Echiurus uncinatus*.

Standing out from the vesicle-wall are many ciliated funnels (Pl. 10. fig. 35, *f.*), on the structure of which I have nothing new to add.

The vesicles are held in position by fine muscular fibres which attach them at various points to the body-wall, but apart from this they float freely in the body-cavity beyond their point of union with the rectum. Pl. 10. fig. 36 shows a transverse section of the body at a point where the vesicles open—ventro-laterally—into the rectum, each through a strikingly small aperture (*a*<sup>1</sup>, *a*<sup>2</sup>); but according to some authors it is doubtful if this should be looked upon as being a true part of the alimentary canal, or if it is not rather an invaginated portion of the epidermis. There is, beneath the anal epithelium in this region, a belt of peculiar tissue which, in this species, extends forwards beyond the openings of the anal vesicles; it has been thought to be modified glandular tissue belonging to the epidermis, in which case the vesicles in *Echiurus uncinatus* would open on the external surface which has become secondarily internal. This special tissue has been described by Spengel as “glandular”; in all my preparations, however, it appears to be a highly vacuolated connective tissue, differing from the ordinary connective tissue only in possessing fewer fibrous elements and fewer nuclei (Pl. 10. fig. 37, *t.p.*; *t.a.*); the striking feature connected with this tissue is the abruptness with which it passes over into the typical connective tissue (*t.a.*), as is seen in fig. 37, where both types occur side by side in one fold of the rectum-wall. The epithelium covering these different tissues is the same, possessing, in both cases, an abundant supply of unicellular glands, whose nuclei are situated at the basal ends of the cells; many of these gland-cells sink down into the tissue beneath, where they are seen cut across in all positions. Apart from these glandular elements belonging to the epithelium, this special tissue gives no evidence in support of the view that it is “glandular.” What is its real significance is a physiological problem which must be worked out on fresh or living material before it can be settled satisfactorily. It is, however, probable that this animal performs some kind of anal respiration, and that this area of vacuolated tissue is connected with the intake of fresh sea-water, becoming alternately turgid and flaccid. The significantly large supply of radiating muscles on the rectum near the anus also suggests a suction action, such as takes place in the rectum of a Holothurian, where there occurs a similar series of muscles. In the straight posterior or rectal portion of the alimentary canal of *Echiurus uncinatus* (Pl. 7. fig. 5, *r.*) one finds two parasites—*Trichodina* and a Copepod, and of these I hope later on to write a separate account. In all probability they enter “per anum,” for had they, or their eggs or spores, been taken in orally, they would undoubtedly have been digested before reaching that part of the alimentary canal

in which they live; it therefore seems likely that they are admitted to the rectum in a stream of water, having a respiratory significance, and taken in through the anal sphincter. The most satisfactory preparations of this tissue were those treated in bulk with alum-carmines, having first cleared the tissue of corrosive-sublimate crystals by immersing it for an hour in iodine solution. I found a sort of precipitate was thrown down in preparations treated in bulk with Ehrlich's hæmatoxylin, followed by a stain for a few minutes on the slide of a slightly acid solution of Grüber's Orange G in 70 per cent. alcohol; but otherwise these formed very excellent contrast stains.

Spengel says of *Echiurus Pallasii* that the vesicles open exactly on the line of demarcation between what he calls the "drüsenlosen" and the "drüsenreichen" areas; so that regarding the "glandular" tissue as epidermal, the vesicles in this case open neither internally nor externally, but on the boundary. According also to Rietsch: "L'orifice des glandes anales serait exactement à la limite entre les téguments et l'intestin." The study of the development of the Gephyrea, according to Korschelt and Heider\*, proves that these organs "do not arise, as was supposed, from the intestine, but are formed in the somatic layer of the mesoderm"; and further that "their entire mode of origin proclaims the anal vesicles to be nephridia which only secondarily entered into connection with the hind gut." If this is so, their function must be excretory; and the observations of many zoologists lend support to this theory. For instance, Shipley says: "The function of these structures may be excretory; or they may control the amount of liquid." Danielssen and Koren†, speaking of the anal vesicles of *Hemingia arctica*, assign to them the function of nephridia, denying the possibility of their having a respiratory significance, for they do not think the sea-water penetrates into the vesicles.

Rietsch observes: "Quant aux fonctions de ces organes, je crois, avec H. de Lacaze, qu'elles sont avant tout glandulaires, excrétoires. Les courants déterminés par les cils des entonnoirs, de la glande elle-même et de la portion terminale de l'intestin, ne peuvent donner naissance qu'à un courant vers l'extérieur. Les glandes, en se distendant, ne déterminent elles pas, malgré ce courant, la pénétration, à l'intérieur de la glande, de l'eau de mer qui servirait ainsi à la respiration du liquide de la cavité générale? 'A priori,' la chose n'est peut-être pas impossible, mais l'observation directe pourrait seule prouver qu'elle a réellement lieu. Il ne semble pas, en tout cas, que cette eau puisse par les entonnoirs aller se mêler au liquide périviscéral, surtout chez l'*Echiure* et la *Thalassème*. En somme les fonctions respiratoires des glandes anales demeurent douteuses."

Huxley, Gegenbaur, Claus, and Hatschek consider the anal vesicles as homologues of the segmental organs of worms.

Other investigators, however, have looked upon them as being undeniably respiratory in function. Greeff, in his account of these organs in the Echiurids, begins by saying: "Als Respiration-organe müssen in erster Linie die beiden Analschläuche betrachtet

\* Text-book of Embryology—Invertebrates, vol. i. p. 309.

† "Fra den norske Nordhavs Expedition (Gephyreer)," *Nyt Mag. f. Nat. Vid.* vol. xxvi. pp. 44-66.



werden, Kiemen im vollen Sinne der Wortes, völlig den analog sogenannten 'Wasserrungen' der *Holothurien*." Schmarda's\* opinion coincides with this, and Forbes and Goodsir's† went the length of calling the anal vesicles "Athemsäcke."

There may be rectal respiration, but it is extremely doubtful if the anal vesicles act as lungs, for though there be a current of water in and out of the anus, it cannot possibly flow freely through the vesicles, their structure rendering this impossible. In the first place, the apertures leading into the vesicles from the rectum are too small to allow of any appreciable amount of water entering them; but allowing that the water does penetrate to the vesicles, it cannot get further, for the ends of the ciliated canals (described minutely by Spengel in *Echiurus Pallasii*) would act as valves, completely preventing the passage of any liquid into the body-cavity; lastly, the cilia in the canals are directed inwards, as Spengel and Greeff both remark, which is conclusive evidence that fluid may be carried from the body out at the anus but not in the opposite direction.

It, therefore, appears probable that the function of these organs is excretory; the granule-containing cells in the walls of the vesicles may function as carriers which collect waste matter, and throw it and themselves away. The vesicles are full of body-cavity fluid, which may be the product of the ordinary cells forming the peritoneal lining of the coelom; for in no part of the animal is there any glandular tissue like the chloragogenous tissue in *Lumbricus* which secretes the coelomic fluid in that worm. It has been suggested that the anal vesicles secrete the coelomic liquid, though, so far as I can judge from my observations in *Echiurus uncinatus*, there is no evidence to support such a view.

*Segmental Organs*.—Posterior to the two anterior ventral setæ are two pairs of nephridia, or segmental organs (Pl. 7. figs. 5, 12, *o.s.*), opening on the one hand into the body-cavity, and on the other to the exterior. The lips of the inner opening are produced out right and left into long tapering arms (Pl. 7. fig. 12, *l.s.*), which are spirally grooved and densely ciliated, but which contain no canal. Drasche says there are 20–30 coils in each spiral arm; but in taking the average among many of my specimens, I find it is less than this, there being not more than 12–20 coils. At the base of these arms, and exactly between them, is the aperture leading into the vesicle from the body-cavity (Pl. 9. fig. 25; Pl. 10. fig. 38, *ap.*<sup>2</sup>); the contents of the vesicle are discharged externally through a minute pore in the body-wall (*ap.*<sup>1</sup>). Pl. 9. fig. 25 represents a section through the entire body of the worm, and in it are seen the two openings of the vesicle (*ap.*<sup>1</sup>, *ap.*<sup>2</sup>), the spiral arms (*l.s.*), and the vesicles containing ova.

In some individuals the vesicles, being highly muscular, are enormously distended by the mass of reproductive products contained in them; they stretch back some way among the coils of the alimentary canal, when they are in this inflated condition—this is also the case in *Bonellia* (Greeff).

Each vesicle possesses but one chamber, whereas in *Bonellia* it is divided into two by

\* Zur Naturgesch. der Adria: 1. *Bonellia viridis*, pls. 4–7, in Memoire of the Acad. of Vienna, 1852, vol. ii.

† "On the Natural History and Anatomy of *Thalassema* and *Echiurus*," Edin. New Phil. Journ. 1841, vol. xxx. pl. vii.



a partition. The inner surface of the vesicle is not ciliated, for the cilia on the spiral arms do not continue in beyond the canal leading into the vesicle—in this canal the cilia are directed inwards towards the interior of the vesicle. As Drasche has already pointed out, there are two bands of longitudinal muscles attaching the segmental organs to the body-wall.

These nephridia have been looked upon by some authors as reproductive organs, and Pallas\* named them “vesiculæ genitales”: this error must have arisen from the fact that they function as gonoducts, though they serve only as temporary receptacles for the reproductive products. They are typical nephridia; and Rietsch says: “Les poches génitales des Échiurens sont évidemment homologues des organes segmentaires des Annélides.” They have much systematic significance; and differences in the excretory organs form important distinguishing features among the various species and genera of the Gephyrea. Drasche gives as one of the characteristic marks of *Echiurus uncinatus* “die mit Spiralrinnen versehenen Trichter der Segmentalorgane.”

*Reproductive Organs.*—In mature individuals the ova or spermatozoa are found floating freely in the cœlomic fluid: there are no special gonoducts, but the segmental organs perform the function of transmitting the ripe sexual products from the cœlom to the exterior. The sexes are separate in this species, though there is apparently no sexual dimorphism, such as occurs, for example, so strikingly in *Bonellia viridis*.

The ova and spermatozoa are the product of the peritoneal cells lining the body-cavity, in one localized area—i. e., along the ventral surface, around the ventral nerve-cord, chiefly at the posterior end of the body-cavity; they are formed by a proliferation of the peritoneal cells in this region. When the sexual cells are ripe they become budded off into the cœlom, where they float about in the perivisceral fluid until they escape to the exterior through the segmental organs. In microscopic sections of the proboscis, ova are present in the sinuses almost at the tip of that organ, showing beyond question that these sinuses are merely forward extensions of the cœlom, and are not blood-vessels.

Greeff pictures the genital cells as budding off from a stem or rhachis; Spengel says this axis is formed from the posterior extremity of the ventral blood-vessel: “Die Stiele scheinen rundum vom einem gemeinschaftlichen Strang, einer gemeinschaftlichen Rhachis, hervorzusprossen.” Greeff and Spengel call this an “ovary.”

The ova are, comparatively speaking, large; they are dark and granular, with the egg in the centre as a clear spot or vacuole; there is an egg-membrane or shell.

The spermatozoa—of typical form with a globular head, and a flagellum-like tail—float in the cœlom in little balls or heaps.

*Mesenteries.*—Several members of the class Echiuroidea possess definite mesenteries; and many zoologists have attached great importance to these structures, claiming for them a systematic significance, inasmuch as they are supposed to be indicative of primitive segmentation, of which almost all trace is wanting in the adult. This is the view put forward by Spengel in his observations on *Echiurus Pallasii*. Referring to the septum-like membrane in the region of the pharynx, he says:—“Dieses Diaphragma ist eine dünne, durchsichtige, von feinen Muskelfäden durchzogene Membran, die sich vor

\* *Miscellanea Zoologica*. Hagæ Comitum, 1760.

[illegible]

Wolke, describing the observed signs of female rats, says: "It's all an attempt to be pregnant because it's the only way to spend the winter." According to Wolke, the ground squirrels of the Sonoran desert (Mammals of the Sonoran Desert) are not the only ones that do this.

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**Abstract of the contents of the following pages is given in a separate publication: The book contains full text of the following: 1. Introduction; 2. Chapter 1; 3. Chapter 2; 4. Chapter 3; 5. Chapter 4; 6. Chapter 5; 7. Chapter 6; 8. Chapter 7; 9. Chapter 8; 10. Chapter 9; 11. Chapter 10; 12. Chapter 11; 13. Chapter 12; 14. Chapter 13; 15. Chapter 14; 16. Chapter 15; 17. Chapter 16; 18. Chapter 17; 19. Chapter 18; 20. Chapter 19; 21. Chapter 20; 22. Chapter 21; 23. Chapter 22; 24. Chapter 23; 25. Chapter 24; 26. Chapter 25; 27. Chapter 26; 28. Chapter 27; 29. Chapter 28; 30. Chapter 29; 31. Chapter 30; 32. Chapter 31; 33. Chapter 32; 34. Chapter 33; 35. Chapter 34; 36. Chapter 35; 37. Chapter 36; 38. Chapter 37; 39. Chapter 38; 40. Chapter 39; 41. Chapter 40; 42. Chapter 41; 43. Chapter 42; 44. Chapter 43; 45. Chapter 44; 46. Chapter 45; 47. Chapter 46; 48. Chapter 47; 49. Chapter 48; 50. Chapter 49; 51. Chapter 50; 52. Chapter 51; 53. Chapter 52; 54. Chapter 53; 55. Chapter 54; 56. 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Black apparently has not called the "College" in Brown School, to the only extent he seems to associate it to school: "The Association for Black Psychology and Blackology will be holding their annual meeting and I intend to give a talk and make an address at some point."

Danielssen and Koren, in *Epithetosoma norvegicum*, speak of a ventral mesentery; though Sedgwick\*, referring to the Echiuroidea as a whole, says "there is no special mesentery, but strands of tissue run from all parts of the body-wall across the body-cavity, to be inserted into the walls of the alimentary canal."

Jameson, however, in his recent paper on *Thalassema neptuni*, recognizes a dorsal mesentery running along the whole course of the alimentary canal except on the gizzard, and a ventral mesentery, "bearing the ventral vessel throughout its entire length, is attached to the alimentary canal anteriorly and posteriorly." . . . "At the hinder end of the œsophagus it suddenly leaves the digestive tube with a falciform free margin and extends as a short free fold along the ventral surface, attached to the peritoneal sheath of the nerve-cord and bearing the ventral vessel. Posteriorly it approaches the gut again, and attaches itself to the cæcum, on the walls of which the solid continuation of the ventral vessel ends." . . . "Owing to the presence of the web of ventral mesentery which occupies the œsophageal loop, the gut, with the two mesenteries, shuts off a portion of the body-cavity forwards, forming a kind of false diaphragm. This anterior division of the body-cavity opens out by a single small hole through which the ventral, and at times the dorsal, blood-vessel passes forwards; this aperture is bounded by a small piece of the left ventral body-wall which lies between the insertion of the dorsal mesentery and the nerve-cord." . . . "The radially arranged folds of peritoneum around the mouth and anus are quite irregular and consequently call for no attention." I dissected *Thalassema neptuni* and *Echiurus Pallasii* in order to see the mesenteries, and conclude that what Jameson calls "a kind of false diaphragm" corresponds to what Spengel calls the "diaphragm" in *Echiurus Pallasii*. But in *Echiurus uncinatus* there is no structure comparable with either of these membranes; the only mesenteries are irregular strands attaching the alimentary canal and anal vesicles to the body-wall, and the radiating mesenteries on the rectum and buccal sac. Pl. 10, fig. 39, is a drawing of the worm as it appears when first opened with the alimentary canal not yet uncoiled; obviously the arrangement of the mesenteric strands is quite irregular and indefinite (*s.m.*). The arrangement of the peritoneal folds on the buccal sac is shown in fig. 1, p. 91, where many of the dorsal attachments are shown cut through. Figs. 40-43 are drawings of a series of sections cut through the anterior end of the body, in which the radial folds appear in transverse section; they are most numerous dorsally, fixing the pharyngeal portion of the alimentary canal firmly to the body-wall.

As regards mesenteries, therefore, it appears that *Echiurus uncinatus* differs widely from *Echiurus Pallasii* and *Thalassema neptuni*. There is no indication of segmentation that I can see, in the structure of the adult of this Japanese *Echiurus*; as to its probable relationship with the segmented worms, that is a question which can only be settled after a careful study has been made of the development of this and allied species, and by following the fate of the larval organs. It is known in the trochophore larva of *Echiurus* that the pair of mesoblastic bands become segmented up into 15 pairs of mesoblastic somites, though, so far as is known at present, no segmentation occurs in the larva of *Bonellia*.

\* Student's Text Book of Zoology, vol. i. 1898, p. 529.

Sedgwick regards the Echiuroidea "as Annelids in which segmentation is feeble, showing faintly in the young, but, except in the repetition of the nephridia, . . . being absent in the adult."

*Proboscis*.—The proboscis is essentially characteristic of the Echiuroidea, usually being a long highly contractile organ, which, when fully extended, assumes an almost ribbon-like form. This prostomium is formed from the oral and præ-oral parts of the larva.

According to Greeff, the proboscis functions as a lung, the blood in its vessels being separated from the sea-water only by a very thin layer of tissue; it thus becomes oxygenated and, as he thinks that a communication exists between the blood-system and the cœlom at the tip of the proboscis, the body-cavity fluid in this way becomes aerated at the same time. Spengel, as I have elsewhere remarked, denies the existence of this open communication, and Rietsch says he has been unable to find it. As regards the proboscis serving as a respiratory organ in *Bonellia viridis*, L., Rolando \* says: "es ist kein Anzeichen da, dass er ihm zum Athem oder als Kieme diene." Schmarda agrees with Greeff in thinking that the respiratory function is carried on by the proboscis and the anal vesicles. It seems doubtful, to my mind, whether the proboscis functions as a lung, if only on account of the well-known fact that it is completely thrown off on the slightest provocation: if it subserved such an important function as respiration, it seems scarcely probable that the animal could so readily part with it; yet in the specimens of *Echiurus Pallasii* which I have examined (obtained from St. Andrews) the proboscides were missing, leaving in each case a scar round the mouth.

Greeff also assigns to the proboscis the function of prehension of food material, by definitely seizing the prey and rolling it into the mouth; but Spengel thinks this is done by the cilia on the ventral surface, apart from any action of the organ as a whole. The proboscis of *Echiurus uncinatus* differs widely from that of allied forms: it is very small, thick, and blunt, being scarcely more than a præ-oral lobe (fig. 2), and in this species it is difficult to see how it can act as a lung or for the prehension of food. Doubtless it is much contracted in these preserved specimens, but, even allowing for that, it is an extremely insignificant organ compared with that of *Echiurus Pallasii*, *Thalassema*, and *Bonellia*. If its insignificance were due to great contraction, then the lateral nerve-cords would be thrown into deep folds, as is the ventral cord; but on dissecting out the nerve-ring in the proboscis-tissue (Pl. 9. fig. 27) it is seen to be very slightly wavy, which points to the fact that the proboscis cannot be extended far beyond its condition in my specimens (Pl. 7. figs. 1, 2). There is no proboscis in the aberrant genus *Saccosoma*, described by Danielssen and Koren.

The ventral surface is entirely clothed with cilia, which are not restricted to a groove.

The sinuses, which are so conspicuous in the tissue of the proboscis, as seen in transverse sections, I have already referred to when considering the "blood-vascular system." There may, however, be some correlation between the development of the blood-vascular system and the proboscis. It is known that, in those larvæ of the Gephyrea whose development has been followed, the vascular system is formed late, and

\* Isis von Oken, i. 1823, Taf. v. figs. 1 5.

its nature seems to be entirely different from that in other animals. In the adult it functions less as a circulatory system than as a hydraulic apparatus for expanding the proboscis in the Echiuroidea, and the tentacles in the Sipunculoidea, where it is entirely absent from the following forms, which have no tentacles: *Petalostoma*, *Onchnesoma*, and *Tylosoma*. Similarly here, in *Echiurus uncinatus*, the absence of the vascular system may be in direct correlation with the extreme reduction of the proboscis. This view gains some support from the fact that in the Priapulidea, an allied group, where there are no head appendages (such as proboscis or tentacles), there is no vascular system.

Mr. Shipley \* has called my attention to the fact that *Thalassema vegrande*, Lampert, has no proboscis, and but for the hooks there is no external indication as to which is the anterior end.

*Distribution and Affinities.*—Up to the present this species has only been met with on the Japanese coast; this is evidently the worm Willemoes-Suhm found there in great abundance, and Drasche's two examples were collected by Dr. A. von Roretz on the east coast of S. Japan; my specimens came from Tokyo.

The affinities of the Echiuroidea, as a whole, are doubtful, and different zoologists classify them very differently. Korschelt and Heider, after studying the development of the group, say that, "as regards the position of the Echiuridæ, we agree with Hatschek's † view; he sees in them a division of the Annelida, and brings them in relation with the Chætopoda. The form and internal organization of the larva, as well as the mode of origin of the setæ, seem fully to substantiate this view. Even though the segmentation (metamerism) no longer exists in the adult animal, it was nevertheless established in the larva, just as in the Chætopoda and Archiannelida. The loss of the segmentation and the reduction of the setæ, as well as the enormous extension of the prostomium, or so-called proboscis, make the Echiuridæ appear as somewhat modified forms." This is confirmed by Conn ‡, who, with Hatschek, inclines to separate the Echiuroidea from the Sipunculoidea. Shipley, however, is of opinion that the resemblances between these two great classes outweigh the differences, and that the Echiuroidea are derived from the Chætopoda, the nearest ally being *Sternaspis*; that the Sipunculoidea are also allied, but have departed much further from the Annelid stock. My observations on this Japanese Echiurid lead me to believe that the connection with the Sipunculoidea is slight, and that the features which separate the two classes are fundamental.

As regards the affinities of this species with the other members of the genus, there are several very important points of difference, which may even justify its being placed in a new genus by itself:—(1) Unlike all other known genera of the Echiuroidea—with the exception of the aberrant *Saccosoma*—it has no extensible proboscis, that organ being represented merely by a short blunt prostomial lobe (Pl. 7. fig. 2); (2) according to Shipley, a closed vascular system is characteristic of all Echiurids, yet it is totally absent here—this may be indicative of a very primitive condition, but, apart from that, it is, I think, a

\* "Report on the Gephyrean Worms collected by Mr. J. Stanley Gardiner at Rotuma and Funafuti," Proc. Zool. Soc. 1898, p. 472.

† "Ueber Entwicklungsgeschichte von *Echiurus*, etc.," Arbeiten zool. Inst. Wien, Bd. iii. 1881.

‡ "Life-history of *Thalassema*," Stud. Biol. Lab., Johns Hopkins University, Baltimore, vol. iii. 1886.

character of generic importance; (3) the presence of a very definitely marked belt of compound glands in the skin is a feature peculiar to this species, (4) as is also the single circlet of peri-anal hooks, and (5) the spiral arms of the inner funnels of the segmental organs; (6) there is also no special mesentery nor diaphragm such as occur in *Echiurus Pallasii* and *Thalassema neptuni*; and the alimentary canal seems to be simpler, for I cannot distinguish the various regions named by Spengel, Jameson, and others.

These peculiar features seem to me to have more than specific significance, and may make it advisable to place this Japanese worm in a separate new genus. On making dissections of *Echiurus unicinctus* and *Pallasii*, and *Thalassema neptuni*, the identity between the two latter was very striking, the only fundamental difference being that *Thalassema* has no peri-anal bristles, its blood-system, proboscis, mesenteries, nephridia, body-wall, and alimentary canal all showing close agreement with *Echiurus Pallasii*; whereas, in these numerous and important respects, the Japanese "species" is utterly unlike the British Echiurid. Drasche, however, says "dieser neue *Echiurus* verbindet also Merkmale von *Thalassema* mit denen von *Echiurus* und erweitert somit nicht allein die bisherigen Anschauungen über der Bau der Segmentalorgane bei *Echiurus*, sondern modificirt auch durch seinen nur einfachen Hakenkranz die Umgrenzung der Gattung selbst, wie sie bisher angenommen werden." His examination of the species, however, was limited to two specimens, and was necessarily not exhaustive; but after the facts which have now come to light it would be necessary to extend the limits of the genus very considerably, if the species *unicinctus* is to be retained within it.

## EXPLANATION OF THE PLATES.

### PLATE 7.

- Fig. 1. *Echiurus unicinctus* (natural size).  
 2. Ventral view of the anterior extremity (enlarged).  
 3. Anterior seta, side view.  
 4. Piece of the external surface (magnified), showing the papillæ elongated transversely.  
     ↑ A=anterior.   ↓ P=posterior.  
 5. Lateral dissection; alimentary canal displaced.  
 6. Longitudinal section through the body-wall in the region of the segmental organs.  
 7. Section through a compound gland (highly magnified).  
 8. Transverse section through the body-wall in the middle of the worm.  
 9.     "         "         "         "         "         at the posterior end of the worm.  
 10. Longitudinal muscle-fibres of fig. 9, more highly magnified.  
 11. Section through a papilla on the proboscis, showing a group of sensory cells.  
 12. Dissection of the anterior end, showing the absence of blood-vessels and of the "diaphragm or septum" which occurs in *E. Pallasii*.



## PLATE 8.

Fig. 13. Diagrammatic section through the mouth.

- 14. " " " pharynx.
- 15. " " " crop.
- 16. " " " gizzard.
- 17. " " " intestine.
- 18. " " " rectum.

13 a. [Drawn with the camera lucida.] Detailed drawing of part of fig. 13.

14 a. " " " " " " " fig. 14.

17 a. " " " " " " " fig. 17.

18 a. " " " " " " " fig. 18.

19. Alimentary canal where the collateral intestine arises.

20. " " " " " ends.

21. " " opened, showing the aperture leading into the origin of the collateral intestine.

21 a. Transverse section through the intestine and collateral intestine.

21 b. " " " ciliated groove.

## PLATE 9.

Fig. 22. [Drawn with the camera lucida.] Transverse section of the body on a level with the basal muscle of the setæ.

23. [With camera lucida.] Transverse section of the body at the nerve bifurcation.

24. " " " " " " " showing the sinuses of the proboscis opening out as the cœlomic cavity.

25. [Drawn with the camera lucida.] Transverse section of the body where the segmental organs open interiorly and exteriorly.

26. [Drawn with the camera lucida.] Transverse section through the prostomium.

27. Dissection of the buccal loop ("œsophageal loop") of the nervous system.

28. Transverse section of the ventral nerve-cord.

29. Part of same, more highly magnified.

30. Longitudinal section of the nerve-cord.

31. Dorsal region of a trans. sect. through the ventral nerve-cord of *Lumbricus*.

32. " " " " " " " *E. uncinatus*.

## PLATE 10.

Fig. 33. Piece of contracted anal vesicle.

34. Section through same.

35. Surface view of a contracted vesicle (carm. alum; clarified in oil of cloves).

36. [Camera lucida drawing.] Trans. sect. of posterior end of the body, where the anal vesicles open into the rectum.

37. [Camera lucida drawing.] Section of one fold of wall of rectum, anterior to the opening of the anal vesicles, showing the two kinds of tissue (stained in bulk with carm. alum).

38. Longitudinal section through a segmental organ with its openings.

39. *E. uncinatus* when first opened, with its viscera "in situ," showing the distribution of the mesenteric strands.

40-43. Series of transverse sections through the body, showing the radial arrangement of the mesenteric strands. The cœlom gradually passes over into the sinuses of the proboscis.

*Reference Letters.*

- |   |  |
|---|--|
| <i>a.</i> , anus.   | <i>m.b.</i> , basal muscle between the setæ. |
| <i>a.</i> <sup>1</sup> , } apertures between the vesicles and | <i>m.c.</i> , circular muscle.               |
| <i>a.</i> <sup>2</sup> , } rectum.                            | <i>m.l.</i> , longitudinal muscle.           |
| <i>ap.</i> <sup>1</sup> , exterior opening.                   | <i>m.o.</i> , oblique muscle.                |
| <i>ap.</i> <sup>2</sup> , interior opening.                   | <i>n.</i> , ventral nerve-cord.              |
| <i>c.</i> (figs. 6, 25), cuticle.                             | <i>nc.</i> , nuclei.                         |
| <i>c.</i> , nerve-cells.                                      | <i>n.l.</i> , lateral nerve.                 |
| <i>c.b.</i> , buccal-nerve commissure.                        | <i>nu.</i> , nucleus.                        |
| <i>c.c.</i> , ciliated canal.                                 | <i>o.</i> , ova.                             |
| <i>c.d.</i> , dense layer of cuticle.                         | <i>c.</i> (fig. 21), aperture.               |
| <i>c.g.</i> , gland-cell.                                     | <i>o.s.</i> , segmental organ (vesicle).     |
| <i>c.n.</i> , "neural canal."                                 | <i>p.</i> (fig. 1), papillæ.                 |
| <i>cr.</i> , crop.  | <i>p.</i> , peritoneum.                      |
| <i>c.s.</i> , sensory cells.                                  | <i>pb.</i> , proboscis.                      |
| <i>c.v.</i> , vacuolated layer of the cuticle.                | <i>ph.</i> , pharynx.                        |
| <i>d.</i> , diverticula.                                      | <i>pp.</i> , granular protoplasm.            |
| <i>e.</i> , epidermal cell.                                   | <i>r.</i> , rectum.                          |
| <i>e.g.</i> , glandular epithelium.                           | <i>s.</i> , secretion.                       |
| <i>ep.</i> , epithelium.                                      | <i>s.a.</i> , anterior seta.                 |
| <i>f.</i> , ciliated funnel.                                  | <i>s.d.</i> , dorsal sinus.                  |
| <i>f.c.</i> , canal of funnel.                                | <i>s.m.</i> , mesenteric strands.            |
| <i>fm.</i> , muscle-fibres.                                   | <i>s.p.</i> , posterior seta.                |
| <i>fn.</i> , nerve-fibres.                                    | <i>s.v.</i> , ventral sinus.                 |
| <i>g.</i> , compound glands.                                  | <i>t.a.</i> , ordinary tissue with fibres.   |
| <i>g.c.</i> , ciliated groove.                                | <i>t.c.</i> , connective tissue.             |
| <i>gr.</i> , granule-containing cells.                        | <i>t.p.</i> , so-called "glandular" tissue.  |
| <i>g.u.</i> , unicellular gland.                              | <i>v.</i> , cavity of vesicle.               |
| <i>g.z.</i> , gizzard.  | <i>v.a.</i> , anal vesicle.                  |
| <i>i.c.</i> , collateral intestine.                           | <i>v.c.</i> , ciliated ventral surface.      |
| <i>l.s.</i> , spiral lip.                                     | <i>w.</i> , body-wall.                       |
| <i>m.</i> , mouth.  |  |



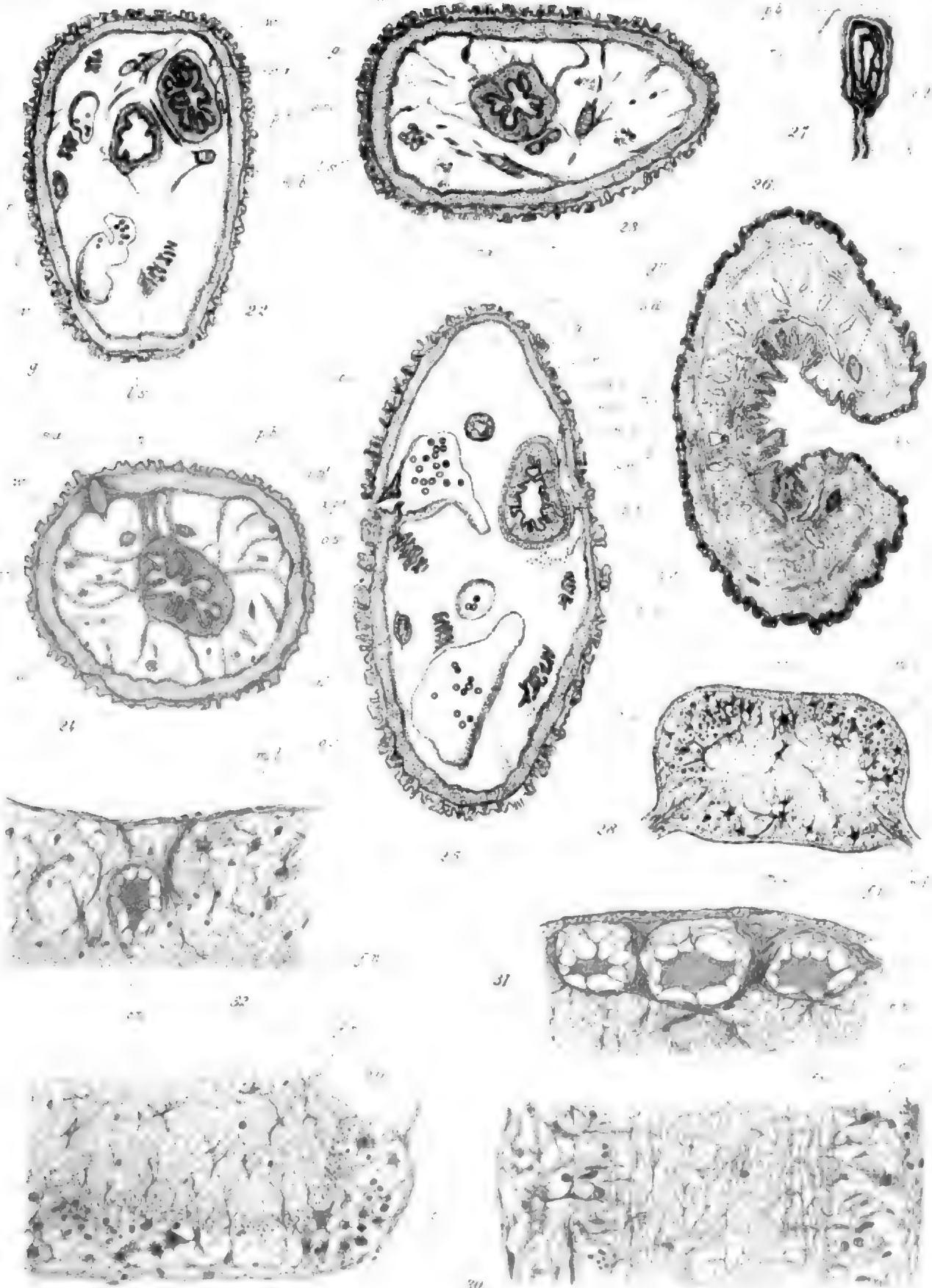
FIG. 1.

FIG. 2. (continued)

FIG. 3. (continued)



ECHINURUS UNICINCTUS



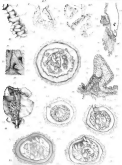


PLATE 10.

MICROSCOPICAL SOCIETY.

PLATE 10.



IV. *The Terrestrial Isopoda of New Zealand.* By CHARLES CHILTON, *M.A.*,  
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(Plates 11-16.)

THE first Terrestrial Isopoda described from New Zealand were those given by Dana \* in 1853, in his account of the Crustacea collected by the United States Exploring Expedition; in it he described and figured in considerable detail 7 species (including one doubtful one), all of them from the northern part of New Zealand. In 1865 one or two species were added by Heller † in the report on the Crustacea of the Novara Expedition. In 1876 Mr. E. J. Miers ‡ compiled a Catalogue of the New Zealand Crustacea, and in connection therewith described some new species that were in the collections of the British Museum; he added 5 species, and his catalogue contains altogether 12 species and one considered doubtful. During subsequent years a few species were added by Mr. G. M. Thomson § and myself ||, and all the species known were included in our "Critical List of the Crustacea Malacostraca of New Zealand." ¶ In 1885 Budde-Lund \*\* published his "Crustacea Isopoda Terrestria," and added two new species and mentioned most of those previously described, but as he was unable to examine specimens he could give no additional information on them, and was obliged to leave several of them under the heading of "uncertain species." Four other new species were described and figured by Filhol in 1885 in his "Mission de l'île Campbell," †† in which he also gave references to previously described species.

In the present paper I endeavour to give a complete list of all the New Zealand Terrestrial Isopoda at present known, with descriptions of the various species and figures where necessary. The material at my disposal consists chiefly of collections that I have accumulated since 1884. Besides specimens that I have collected myself, I have many from Mr. R. Helms, formerly of Greymouth, Mr. J. McMahon, of Kenepuru, Mr. W. W. Smith, of Ashburton, Mr. S. H. Drew, of Waunganui, Mr. H. Suter and Mr. R. M. Laing, of Christchurch, and Mr. L. Hames, of Takapuna. Mr. G. M. Thomson has very kindly placed in my hands the whole of his collection, including

\* J. Dana: U. S. Exploring Expedition, Crustacea, vol. ii. pp. 713 *et seqq.* (1853).

† Cam. Heller: "Reise der Novara," Zool. Bd. 2, pp. 134-136 (1865).

‡ E. J. Miers: *Annals & Mag. Nat. Hist.* (ser. 4) xvii. pp. 225-227 (1876); and *Catalogue New Zealand Crustacea*, pp. 94-102 (1876).

§ G. M. Thomson: *Trans. N. Z. Inst.* xi. p. 232 & p. 249 (1879); and *Annals & Mag. Nat. Hist.* (ser. 6) xii. pp. 225-227 (1893).

|| C. Chilton: *Trans. N. Z. Inst.* xv. p. 73 & p. 149 (1883), & xviii. p. 159 (1886).

¶ *Trans. N. Z. Inst.* xviii. pp. 141-159 (1886).

\*\* "Crustacea Isopoda Terrestria," Copenhagen (1885).

†† "Mission de l'île Campbell," *Recueil Mem. Acad. Sci. (Venus)* iii. part 2, pp. 439-446 (1885).

the type specimens of some species described by him. Through the kindness of Professor F. Jeffrey Bell and Mr. R. I. Pocock, I have been able to examine type specimens of Miers' species in British Museum, and Monsieur Adrien Dollfus has sent me species from Europe that have been most useful for comparison. To all these gentlemen I desire to record here my hearty thanks.

Some of the work involved in the preparation of this paper was done in the Natural History Department of the University of Edinburgh, where Professor Cossar Ewart kindly gave me the use of a table, but a large part has been done during vacations in the laboratory of the University College, Dundee, and I desire to record my thanks to Professor D'Arcy W. Thompson, C.B., for the facilities placed at my disposal, and for permission to make free use of the rich stores of Terrestrial Isopoda in the collections under his care, while to Dr. W. T. Calman I am greatly indebted for much kind assistance during the progress of the work.

I have, as far as possible, followed the classification and nomenclature adopted by Professor G. O. Sars in his fine work on the Crustacea of Norway, and have to thank him for sending me the parts bearing on the Isopoda. I have tried to give all the references specially dealing with the New Zealand species, but in the case of species and genera that are also known from elsewhere, I have only given one or two of the most important; for the benefit of workers in New Zealand, where books of reference are few, I have given diagnoses of all the genera, taking these in most cases from Sars' work, and have also given short notes on the characters of the families.

It will be seen that the Terrestrial Isopodan fauna of New Zealand is fairly rich and varied, all the families but one being represented. I am able to give 27 species, belonging to 13 genera, of which only 3 or 4 are "uncertain species"; for the sake of comparison it may be mentioned that in the last list of the Terrestrial Isopoda of the British Isles, as given by Canon Norman\*, there are 20 species, belonging to 11 genera. Moreover, it is probable that the number of New Zealand species will hereafter be increased, especially when the North Island has been thoroughly searched, for at present the majority of my specimens are from the South Island, and only a few more or less haphazard collections have been made in the North Island. Of the outlying islands of New Zealand, I have only two species from Chatham Islands, and one from the Auckland Island. Three species are at present known from single specimens only, and two others have been found only in one locality and on a single occasion. In addition to the species given, specimens from ants' nests, probably belonging to *Platyarthrus*, were referred to by Mr. W. W. Smith, in a paper dealing with some New Zealand Ants, and were stated to have been sent to Europe with other collections from ants' nests. I have endeavoured to trace these specimens, but without success, and so far Mr. Smith has not been able to procure fresh specimens for me.

The Terrestrial Isopoda are well worthy of study from the point of view of the geographical distribution of animals, and the facts of their distribution will be of great value for testing the correctness of the views as to the origin of the fauna of particular

\* Annals & Mag. Nat. Hist. ser. 7, iii. pp. 70-78.

countries and places, for they are strictly terrestrial animals, and as their young are hatched in the incubatory pouch of the female, it seems unlikely that they could cross even comparatively narrow tracts of ocean, except by rare accidents, while a continuous range of high mountains would also be a formidable barrier. In the New Zealand Journal of Science, vol. ii. (1884) p. 155, I have already called attention to the question, and have also pointed out that their distribution in any given land-area may be to some extent influenced by floods in the rivers carrying logs with the Isopods attached to great distances, and have given the following instance where this appears to have actually taken place.

The species *Armadillo regulosus* (= *Cubaris regulosus*, Miers) is common on logs and under the bark of trees in the bush, but I had not found it on the open Canterbury Plains except at one place, Eyreton, where I got numerous specimens under some logs that had been carted for firewood from the river Waimakariri, after having been washed down by the river for at least twenty miles, probably further, from places where the species was abundant. It seems likely that the Isopod had been washed down with the logs, for I found it only at that particular spot at Eyreton, and after the logs had all been used it was no longer seen in that district.

It would, therefore, be interesting if some facts could be given as to the distribution of our New Zealand species, especially of any that may be found in other countries. Unfortunately, however, so little is at present known of the Terrestrial Isopoda of Australia and other lands of the southern seas, that little can as yet be said with certainty.

Of the species, by far the greater part (18) are known only from New Zealand; two species, *Porcellio scaber*, Latr. and *Armadillidium vulgare*, Latr., are cosmopolitan, and have probably been introduced by artificial means; another species, *Philoscia pubescens*, Dana, appears to be identical with a species found at the Cape of Good Hope and at the Seychelles; *Actæcia euchroa*, Dana, is found in Tasmania as well as in New Zealand; while *Ligia nova-zealandiæ*, Dana, and *Oniscus punctatus*, Thomson, are represented in Tasmania by closely allied species, and *Tylos neozelanicus* is probably equally closely related to *T. spinulosus*, Dana, from Tierra del Fuego. In the genus *Trichoniscus* it is rather difficult to make any comparison between the numerous species, but the genus is a very widely distributed one, and species are known from Tristan d'Acunha and Valparaiso\*, and from the Straits of Magellan†. The genus *Armadillo* is represented in New Zealand by at least six species, the greater number of the species of the genus occur in the tropical countries, and Budde-Lund‡ has pointed out that about half of them are from the islands and shores of the Pacific.

Of the distribution and occurrence of the different species in New Zealand itself a little more can be said. Six species (i. e. *Ligia nova-zealandiæ*, *Tylos neozelanicus*, *Scyphax ornatus*, *Actæcia euchroa*, *Actæcia opihensis*, and *Scyphoniscus waitatensis*) are

\* Dollfus: "Isopodes terrestres du 'Challenger,'" Société d'Études Scientifiques de Paris, xiii<sup>e</sup> Année (1890), pp. 5 & 6 (separate copy).

† Stebbing: Proc. Zool. Soc. London, 1900, Part iii. p. 568.

‡ Isopoda Terrestria, p. 16.

littoral, being found on or near the sea-beach, and probably *Scyphax* (?) *aucklandiæ* should also be added to this list. Of these, *Ligia novæ-zealandiæ* is found all round the New Zealand coast, and is very abundant under stones or sea-weed, especially on rocky portions of the shore; *Scyphax ornatus* and *Actæcia euchroa* are found on sandy beaches either on the surface or burying themselves a little in the sand about high water mark or a little lower; *Scyphax ornatus* is probably abundant on all such beaches in the North Island, but in the South Island has, so far, been recorded from Westport only; *Actæcia euchroa* is known from the south as well as the north, and is also found in Tasmania. The remaining littoral species have as yet been recorded each from one locality only.

Of the more strictly terrestrial forms, leaving out of account the two cosmopolitan species *Porcellio scaber* and *Armadillidium vulgare*, and also *Philoscia pubescens*, which is found at the Cape of Good Hope and elsewhere, we have *Oniscus punctatus*, found in all parts of New Zealand; *Armadillo ambiguus* from all parts of the North Island, and from Kenepuru and Greymouth in the South Island, but not known further south; while, on the contrary, *Armadillo rugulosus* and the three species of *Trichoniscus* are widely distributed in the South Island, but as yet not recorded from the North, though in the case of *Trichoniscus* this is no doubt partly owing to their small size. Of the remaining species too little is known to justify any general remark.

It may perhaps be well to mention here a few of what seem to be the more important points brought out in this paper. I have been able to settle, in what I hope will be considered a satisfactory manner, uncertainties that have long existed with regard to several of Dana's descriptions, and in so doing to reduce to the rank of synonyms some species subsequently described (see *Ligia novæ-zealandiæ*, *Scyphax ornatus*, *Philoscia pubescens*, *Armadillo speciosus*): I establish a new family, *Scyphacidae*, corresponding mainly with Dana's subfamily *Scyphacinae*, which had been ignored by most subsequent writers, and show that the imperfect development of the seventh pair of legs, which Dana had considered a character of the genus *Scyphax*, is merely an immature character which in this instance is retained till a later period of life than usual, and settle the question as to the relationship of *Scyphax ornatus* to *Actæcia euchroa* by showing that the only connection between them is that both have the same habit of living on sandy beaches.

In the case of some of the commoner species, I have had numerous specimens from many localities, and have thus been able to make some observations as to the variations that may be met with in these species.

In most of the species there is to be found on the dactylus a specially long and peculiar seta which has characteristic forms in some, at any rate, of the genera. Schiödte figured this "dactylar seta" many years ago in *Titanethes* \* *albus*, and Weber mentioned its presence in some species of *Trichoniscus* †, but I cannot find that any one has drawn special attention to it, though in some cases it is rather noticeable, and together with the form of the dactylus itself, may be of use in readily identifying

\* Bidrag til den underjordiske Fauna (Copenhagen, 1849).

† "Anatomisches über Trichonisciden," Archiv für Mikroskop. Anatomie, Bd. xix, p. 582.

he genus. In *Ligia* the dactylar seta is unbranched and slightly clubbed at the end; in *Trichoniscus* it divides into two branches, each further subdividing into fine filaments; in *Scyphoniscus* it divides similarly, though differing a little in detail; in *Tylos* it is rather short, unbranched, and has the distal half thicker and stippled-looking; in *Acteocia euchrou* it is somewhat similar; while in *Acteocia* (?) *opihensis* it is larger and very distinct, and the stippled appearance of the distal portion looks under a high power as if it were caused by the distal portion, resembling a narrow circular brush with short hairs projecting all round it. It is sometimes lost in specially old and large specimens, but with this exception is always to be found in the genera mentioned; I cannot, however, find it at all in *Scyphax*, *Oniscus*, *Philoscia*, *Armadillidium*, and *Armadillo*. Beyond the suggestion that it is a tactile organ, I can give no information as to its function. A seta, probably also of a sensory nature, is found similarly situated in *Asellus aquaticus* and some other Isopods, and also in many Amphipods, but in these it is less prominent, and does not take such varied forms.

In all the genera, and especially those hitherto imperfectly known, I have examined the mouth-organs in some detail; an accurate knowledge of these will, I think, in time help us on towards a natural classification of this group, for they seem to be much more constant than characters taken from the general shape of the body, from the uropoda, or even from the presence or absence of air-cavities in the pleopoda. It is true that we may get sudden variations in some of the mouth-parts, such as that I have described in the outer lobe of the first maxilla of *Scyphoniscus*, or by Dollfus in the inner lobe of the same maxilla in *Mesarmadillo*; but these, occurring as they do in groups in which the mouth-parts are otherwise very constant, are probably to be looked upon as sudden variations or "sports" that have comparatively little value from a classificatory point of view.

I give here a Table, based mainly on the mouth-parts, showing briefly what appear to be the more important characters of the various families:—

- |  |                |
|--|----------------|
| A. Mandibles with well-developed molar tubercle; inner lobe of 1st maxilla with three plumose bristles.  |                |
| I. Uropoda not concealed under pleon.  |                |
| a. Antennæ with flagellum multiarticulate; eyes large; male organ double . . . . .   | LIGIIDÆ.       |
| b. Antennæ with flagellum not more than 6-jointed; eyes small; male organ single . . . . .   | TRICHONISCIDÆ. |
| II. Uropoda concealed under pleon.   |                |
| a. Segments of pleon separate . . . . .  | TYLIDÆ.        |
| b. First five segments of pleon coalesced . . . . .  | HELLERIDÆ.     |
| B. Mandibles without distinct molar tubercle, its place being taken by a brush-like group of setæ; inner lobe of first maxilla with only two plumose bristles. |                |
| I. Maxillipedes with terminal joints of moderate size; lamellar longer than masticatory lobe . . . . .   | SCYPHAXIDÆ.    |
| II. Maxillipedes with terminal joints small and almost rudimentary, hardly longer than masticatory lobe.   |                |
| a. Uropoda more or less projecting; animals not rolling into perfect ball . . . . .  | ONISCIDÆ.      |

- c. Uropoda not projecting beyond terminal segment; animals rolling into perfect ball . . . . . *ARMADILLIDÆ*.

While this table does not profess to be any very near approach to a natural classification of the Terrestrial Isopoda, it is probable that the two large divisions A and B do represent distinct groups in which development has proceeded on similar lines, in each case leading from animals living on the sea-shore within reach of the waves and breathing only very moist air, to others of pure terrestrial habits capable of breathing ordinary dry air, *i. e.* the Helleridæ in the one case, and the Armadillidæ in the other. It is interesting to notice, too, how the protection afforded by the animal's power of rolling itself up into a ball has been acquired in different groups that are certainly of independent origin, *e. g.* in the Tylidæ, Helleridæ, Armadillidæ, and to a less perfect degree in some of the Scyphacidæ (*e. g.* Actæcia), and perhaps also in some of the Oniscidæ, and how similar is the general appearance of the body in each of these groups, though of course the detailed arrangements by which it is acquired vary. If we go beyond the Oniscoidea, we find a similar power of rolling into a ball and a somewhat similar external appearance in the Sphæromidæ and, among the Myriapoda, in the Gloneridæ.

A tabular arrangement of the Oniscoidea, based on much the same characters as I have used, was given many years ago by Ulianin \*; his table, however, goes into greater detail and separates the genera, and unfortunately it is in the Russian language †.

For the benefit of those who may wish to identify their specimens without going to the trouble of dissecting out the mouth-parts, I give the following artificial key to the New Zealand genera, and a similar key to the species under each genus represented by more than one species:—

- A. Body convex; animal capable of rolling into a ball.
- I. Flagellum of antenna 2-jointed.
    1. Outer branch of uropoda large and terminal . . . . . *Armadillidium*.
    2. Outer branch of uropoda small, inserted on the inner side of the enlarged base. *Armadillo*.
  - II. Flagellum of antenna with more than two joints.
    1. Uropoda quite concealed beneath terminal segment . . . . . *Tylos*.
    2. Uropoda extending beyond terminal segment and visible in dorsal view . . . *Actæcia*.
- B. Body more or less flattened; animal not capable of rolling into a ball.
- I. Flagellum of antennæ many-jointed . . . . . *Lygia*.
  - II. Flagellum 2-jointed.
    1. Side-plates of metasome large, expanded . . . . . *Porcellio*.
    2. Side-plates of metasome small, adpressed . . . . . *Metoponorthus*.
  - III. Flagellum with three to six joints.
    1. Eyes large, crescent-shaped, of many ocelli . . . . . *Scyphax*.
    2. Eyes small, not more than three ocelli.
      - a. Body with longitudinal ridges . . . . . *Haplophthalmus*.

\* 'Crustacea Turkestanica,' St. Petersburg & Moscow, 1875 (see Budde-Lund, *l. c.* p. 12).

† I have to thank Mr. H. A. Webster, Librarian, University of Edinburgh, for translating a portion of Ulianin's work for me.



- b. Body without longitudinal ridges . . . . . *Trichoniscus*.  
 3. Eyes of moderate size, more than three ocelli.  
 a. Pleon with lateral expansions . . . . . *Oniscus*.  
 b. Pleon with lateral expansions.  
 i. Flagellum much shorter than last joint of peduncle . . . . . *Scyphoniscus*.  
 ii. Flagellum about as long as last joint of peduncle . . . . . *Philoscia*.

In the following list 27 species are mentioned, but of these there are 4 which I have not seen, and which must be considered as more or less uncertain, though one, *Armadillo spinosus*, Dana, is in all probability a good species and distinct from the others given, and I have therefore included it in the artificial key to the species. I have not been able to do this with the other three species.

### List of Species.

#### ONISCOIDEA.

##### I. LIGIIDÆ.

1. *Ligia novæ-zealandiæ*, Dana.

##### II. TRICHONISCIDÆ.

2. *Trichoniscus phormianus*, sp. nov.  
 3. „ *otakensis*, sp. nov.  
 4. „ *Thomsoni*, Chilton.  
 5. *Haplophthalmus Helmsii*, sp. nov.

##### III. TYLIDÆ.

6. *Tylos neozelanicus*, sp. nov.

##### IV. SCYPHACIDÆ.

7. *Scyphax ornatus*, Dana.  
 8. „ (?) *aucklandiæ*, G. M. Thomson.  
 9. *Scyphoniscus waitatensis*, nov. gen. et sp.  
 10. *Actæcia euchroua*, Dana.  
 11. „ *opihensis*, sp. nov.

#### V. ONISCIDÆ.

12. *Oniscus punctatus*, G. M. Thomson.  
 13. „ *kenepurensis*, sp. nov.  
 14. „ *Cookii*, Filhol (*not seen*).  
 15. *Philoscia pubescens*, Dana.  
 16. „ *novæ-zealandiæ*, Filhol (*not seen*).  
 17. *Porcellio scaber*, Latreille.  
 18. ? *Metoponorthus pruinosis*, Brandt.

#### VI. ARMADILLIDÆ.

19. *Armadillidium vulgare*, Latreille.  
 20. *Armadillo ambitiosus*, Budde-Lund.  
 21. „ *Danæ*, Heller.  
 22. „ *speciosus*, Dana.  
 23. „ *rugulosus*, Miers.  
 24. „ *monolinus*, Dana (*not seen*).  
 25. „ *Hamiltoni*, sp. nov.  
 26. „ *Macmahoni*, sp. nov.  
 27. „ *spinosus*, Dana (*not seen*).

### Family I. LIGIIDÆ.

In this family the antennæ have the flagellum multiarticulate, *i.e.* with more than six or seven joints, the mandible has a well-developed molar tubercle with triturating surface, the inner lobe of the first maxilla bears three plumose bristles, the terminal portion of the maxillipede is of moderate size and more or less distinctly divided into five joints, and the external male organ is double.

The family contains several genera, the best known being *Ligia*, *Ligidium*, and *Titanethes*. The genus *Geoligia*, Dollfus, appears to be very near to *Ligia*, but the only known species, *G. Simoni*, lives far away from the sea, while all the species of *Ligia* are found on the sea coast.

If *Styloniscus magellanicus*, Dana, belongs to *Trichoniscus* as Stebbing\* thinks, it is evident that the distinction between the Ligiidæ and the Trichoniscidæ as regards the antennæ breaks down, for in that species the antenna may have the flagellum with as many as ten joints. Dollfus, when describing this species, had previously stated that *Styloniscus*, Dana, is very near to *Ligidium*, and differs from it only in the uropods, which want the long hairs characteristic of that genus†; in making this statement, however, he may have had in his mind also the species *Styloniscus gracilis*, Dana, in which the uropoda do resemble those of *Ligidium* as Stebbing has also pointed out, but it is doubtful whether this species is really congeneric with *S. magellanicus*.

In any case the differences between the Ligiidæ and the Trichoniscidæ are not great, and the existence of genera intermediate in characters is only what we may naturally expect.

Dana placed *Styloniscus* in his sub-family Scyphacinæ, but from Stebbing's description of the mouth-parts of *S. magellanicus* it is evident that that species at any rate cannot come under the family Scyphacidæ as I have defined it further on.

#### Genus 1. *LIGIA*, Fabricius, 1798.

*Ligia*, Bate & Westwood, British Sessile-Eyed Crustacea, ii. p. 442 (1868).

*Ligia*, Budde-Lund, Crustacea Isopoda Terrestria, p. 258 (1885).

*Ligia*, Sars, Crustacea of Norway, ii., Isopoda, p. 155 (1899).

The generic characters are given by Sars as follows:—

“Body regularly oval, or oblong oval, moderately convex above, with the metasome not abruptly contracted; last segment rather broad, with distinct epimeral plates. Eyes large and convex. Antennulæ very small, with the last joint rudimentary, nodiform. Antennæ rather strong and elongated. Mandibles with a ciliated lappet and numerous penicils behind the cutting part. Maxillipeds comparatively short and stout, with the terminal part rather expanded, epignath rounded. Legs gradually increasing in length posteriorly, dactylus distinctly bi-unguiculate. Opercular plate of pleopoda sub-branchial. Uropoda more or less elongated, basal part not produced inside, rami narrow, styliform, subequal, each with a single apical spine.”

This is the only genus of the family that is represented in New Zealand, and the single species, *L. novæ-zealandiæ*, described below, agrees well with the characters of the genus as just quoted from Sars. It differs, however, from the characters of the family in that the two hairy bristles on the inner side of the second maxilla are wanting, and the terminal part of the maxillipeds, though showing distinct evidence of five joints, has the three joints preceding the terminal one united together into one plate with the sutures only partially indicated. The external male organs are considerably different from those of the typical species *L. oceanica*. In all these points *L. australiensis*, Dana, from Australia, closely resembles *L. novæ-zealandiæ*, and as these peculiarities are probably shared by other species which like them are nevertheless true *Ligiæ*, it will be well to slightly modify the characters of the family as laid down by Sars in order that these species may be included.

\* Proc. Zool. Soc. 1900, p. 566.

† Mission du Cape Horn, Crustacés, p. 72.

1. *LIGIA NOVÆ-ZEALANDIÆ*. (Pl. 11. fig. 1.)

*Lygia novi-zealandiæ*, Dana, U.S. Explor. Exped. xiv. Crust. part ii. p. 739, pl. xlix. fig. 2 (1853).

*Ligia novæ-zealandiæ*, Miers, Cat. Crust. of New Zealand, p. 103 (1876).

*Ligia quadrata* (Hutton, MS. Cat. N. Z. Crust.), G. M. Thomson, Trans. N. Z. Inst. xi. p. 232, pl. x A, figs. 4 & 4a (1879).

*Ligia novæ-zealandiæ*, Budde-Lund, Crustacea Isopoda Terrestria, p. 271 (1885).

*Ligia quadrata*, Budde-Lund, *l. c.* p. 271 (1885).

*Ligia novæ-zealandiæ*, Filhol, Mission de l'île Campbell, p. 445 (1885).

*Ligia quadrata*, Filhol, *l. c.* p. 445 (1885).

*Ligia neo-zealanica*, Thomson & Chilton, Trans. N. Z. Inst. xviii. p. 157 (1886).

*Ligia quadrata*, Thomson & Chilton, *l. c.* p. 157 (1886).

*Specific description*.—Body elongate oval, about twice as long as broad, rather convex; surface finely granular, sometimes with minute setæ, giving it a punctate appearance. Outer antennæ slender, minutely setose, two-thirds the length of the body; fifth joint of peduncle as long as the third and fourth combined, flagellum fully twice as long as the fifth joint with about twenty joints. Eyes large, subquadrate, distinctly angled towards the middle line, facets very numerous and of small size. Vertex with a transverse depression just posterior to the angle of the eyes, interrupted in the middle.

Posterior border of the first and second segments of the mesosome transverse, not produced backwards at the lateral angles; lateral angles of the remaining segments progressively more and more produced backward, those of the seventh segment reaching as far as the angle of the third segment of metasome. Side-plates ("epimera") large, distinctly marked off from the middle part of the segment by a longitudinal sulcus in the second, third, and fourth segments, the sulcus very indistinct in the remaining segments. Legs spinose, gradually increasing in length posteriorly, the first and second in the male having the carpus broadened, and the propodos and dactylus impinging against it to form a subchelate hand, the first being broader than the second; in the female all the legs simple; in each leg the dactylus has a secondary slender nail about half the length of the terminal nail; at the base of the terminal nail arises on the outer side a long seta slightly clubbed at the end and reaching as far as the end of the terminal nail.

Terminal segment of the metasome subquadrate, its lateral angles acute but not much produced, posterior margin regularly convex in the middle. Uropods with the peduncle subcylindrical, about half the length of metasome; the two rami of nearly equal length, the outer often rather the shorter and more slender, both tapering, minutely setose, and with one or two apical setæ.

Colour: yellowish, closely speckled with black, giving a greyish or slaty effect.

Length about 12 mm., breadth about 5.5 mm.

*Habitat*.—Very abundant on all the coasts of New Zealand, generally found under stones or seaweed about high-water mark, but sometimes extending a little further inland. It runs with great rapidity when disturbed.

*Remarks*.—It is only after considerable hesitation that I have united *Ligia quadrata*, Thomson, with *Lygia novi-zealandiæ*, Dana. When Mr. Thomson described his species he was acquainted with Dana's description, but found that it differed from his specimens

in some points that appeared very definite and well marked, and he therefore established for them the new species *Ligia quadrata*. All specimens subsequently examined, both by Mr. Thomson and myself, were found to agree with the characters as laid down for *L. quadrata*, and thus to differ from *L. novi-zealandiae*, Dana, and hence in our "Critical List of the Crustacea Malacostraca of New Zealand,"\* under the heading *Ligia novi-zealandiae*, the remark is made "I do not know this species, G. M. T." The points in which Dana's description differed from our specimens are:—

- (a) The surface of the thorax and abdomen "covered with very short hairs."
- (b) Base of caudal stylets "nearly as long as the abdomen."
- (c) Branches of caudal stylets "quite unequal" and the longer "hardly as long as the thorax."

In none of the specimens that I have examined could the dorsal surface be said to be "covered with very short hairs," and Mr. Thomson tells me that no hairs are to be found in living specimens, which he has recently re-examined at my request, as I thought it just possible that the hairs might have got worn off in the spirit specimens that I brought from New Zealand with me. I have been anxious to get for comparison specimens from the Bay of Islands, where Dana's type specimens were obtained, and though I have not been successful in this, I have in Mr. Thomson's collection specimens from Waiwera, a locality north of Auckland and not very far remote from the Bay of Islands, and I find that these differ a little from our South Island specimens, and though I regard them as undoubtedly the same species, they show some slight approach towards Dana's description. Thus the antennæ are slightly longer and more slender and distinctly more hairy than in the typical specimens of *Ligia quadrata*, and the surface of the body when viewed with a higher power shows, especially at the edges of the segments, very minute little setæ which, though they scarcely project beyond the surface and are not deserving of the name of "very short hairs," must, I think, have given the appearance which Dana has thus described. In South Island specimens these minute points are much less marked but can occasionally be made out. The uropoda in the Waiwera specimens are a little more slender than in South Island ones, but as in them the base is only about half as long as the abdomen, and I have not seen any in which the base is "nearly as long as the abdomen," but it must be remembered that in young specimens with which Dana perhaps had to deal the uropoda are considerably longer in proportion than in fully-grown specimens. The branches of the uropoda are again usually of nearly the same length, though the outer one is generally a little the shorter, and the variation in their relative lengths is pretty considerable, and specimens in which the difference was more marked than usual may have led Dana to describe them as "quite unequal." The longest branch is, however, always much shorter than the thorax, and I must regard Dana's statement that it is "hardly as long as the thorax" as an unintentional exaggeration or else a mistake for "hardly as long as the abdomen."

In his "Catalogue of the New Zealand Crustacea," Miers refers specimens in the British Museum to Dana's species without any question beyond remarking that "the rami of the caudal appendages are equal except in one specimen, where they are slightly

\* Transactions New Zealand Institute, xviii. p. 157.

unequal." When visiting the British Museum I found, however, that the specimens are labelled "*? Ligia novæ-zealandiæ*, Dana," and that, so far as can be seen in their dried and imperfect condition, they resemble my Waiwera specimens very closely, and thus differ from Dana's descriptions in the other characters that I have pointed out as well as in that of the rami of the uropoda.

I have discussed this question at what will probably be thought to be undue length, but I think that full reasons should always be given before one species is regarded as the synonym of another, and it is well to hesitate before venturing to dispute the accuracy of Dana's descriptions.

As this species is the largest and one of the commonest of the Terrestrial Isopoda of New Zealand, and is, moreover, of a more generalized type than the others, it is deserving of close attention by any who wish to study the group, and I therefore give here a fairly full account of its external anatomy. I do not propose to consider its internal anatomy, though it would no doubt repay careful consideration; indeed, I do not know that the internal anatomy of any species of the genus has yet been worked out in detail, though many years ago Lereboullet published an excellent paper on a species of the closely allied genus *Ligidium* \*, and Max Weber has more recently given a more minute account of the anatomy of some species of the family *Trichoniscidæ* which comes close to the *Ligidæ* †.

*Detailed Description of Ligia novæ-zealandiæ.* (Pl. 11.)

The size is naturally subject to some variation, but all the specimens that I have seen are considerably smaller than fully-grown specimens of *L. oceanica*. The following measurements may be taken as about the average:—length of body 12 mm.; greatest breadth 6 mm.; length of mesosome 7.5 mm.; of metasome 4 mm.; of antennæ 10 mm.; of uropoda 5 mm. (base 2 mm., rami 3 mm.).

The head is oval, about three times as broad as long, the anterior margin regularly convex and without lateral lobes; the eyes are large and occupy nearly the whole of the lateral margins, their anterior and posterior sides meeting at a distinct angle; the facets are small and very numerous.

The surface of the head shows a transverse depression, interrupted in the middle, just posterior to this angle of the eyes.

The first segment of the mesosome is about as long as the head. Its epimeral portions extend anteriorly about to the middle of the lateral margins of the head, the suture marking them off from the central portion being indistinctly marked in posterior part of the segment only; the posterior margin straight; the second and third segments similar but a little longer than the first; the fourth segment the widest, its posterior margin slightly concave, and lateral angles a little produced backwards; fifth, sixth, and seventh segments gradually narrowing; lateral angles acute and more and more produced backwards, those of the seventh segment reaching nearly to the postero-lateral angles of

\* "Mémoire sur la Ligidie de Persoon (*Ligidium Persooni*, Brandt)," Ann. d. Sciences Nat., Seconde Série, tome xx. pp. 103-142, Pl. 4 & 5.

† "Anatomisches über Trichonisciden," Archiv f. Mikroskop. Anatomie, Bd. xix. pp. 579-648, Tab. xxviii.-xxix.

the third segment of metasome. The sutures dividing the epimera from the central portions are fairly evident in the second, third, and fourth segments, but are indistinct in the fifth, sixth, and seventh; in some specimens they are indistinctly marked in the fifth segment also, and the distinctness of the sutures is, I think, a character that is subject to considerable variation, though Dollfus has established a new genus *Geoligia* differing from *Ligia* only in having the epimera not distinct for a species, *G. Simoni*, found in the forests of Venezuela at an altitude of 1200 metres \*.

The metasome is considerably narrower than the mesosome, the first and second segments small and without distinct epimeral projections, third, fourth, and fifth segments subequal with well-developed epimera, lateral angles acutely produced backwards, those of the fifth segment reaching very nearly to the postero-lateral angle of the sixth segment; sixth segment with its posterior margin deeply hollowed on each side for the base of the uropoda, its central part regularly convex.

Surface of whole body slightly granular and with a few irregularities, showing under a high power, especially at the sides, very minute setæ which scarcely project beyond the surface.

The *antennulæ* consist of the usual three joints, the first much the broadest, second nearly as long as the first but narrower, the third very small, rounded at the end; a few minute setæ are present, chiefly on the second joint, but no "sensory setæ" were observed.

The *antennæ* are represented in Pl. 11. fig. 1 a.<sup>2</sup>: the first three joints are subequal, short, nearly as broad as long, the fourth joint shorter than the fifth but broader; flagellum about as long as the last three joints of the peduncle together; in the fig. a.<sup>2</sup>, taken from a specimen 12 mm. in length, the flagellum is composed of fifteen joints, but it may contain a greater or less number, Thomson says "flagellum 16- to 23-jointed." There are numerous short and rather stout setæ on the last three joints of the peduncle, and finer setæ on each joint of the flagellum. In the South Island specimens these latter are usually shorter than the breadth of the joint from which they spring, but in the Waiwera specimens they are fully as long as the joint is wide, or may even slightly exceed this length.

The *mouth-parts* are well developed and of a more generalized type than in most other Terrestrial Isopoda. The *upper lip* calls for no special remark; it is rounded, with a very shallow emargination at its extremity, and provided with numerous short setæ in the usual manner. The *mandibles* are strong and of the same general shape as in *Ligia oceanica*; in the right mandible the outer cutting-edge is formed of four stout teeth; the accessory appendage is slender, bends abruptly about the middle, and on its inner side is prolonged into a slender acutely-pointed process; its terminal part is nearly transparent, and its basal part appears very pale brown and is evidently much less highly chitinized than the corresponding part in the left mandible; between this accessory appendage and the molar tubercle is a soft membranous lobe, rounded at the end and thickly covered with setæ, those along its inner margin being longest and plumose; molar tubercle strong, curving inwards, its truncate extremity covered with closely-set rows of short, stout setæ.

\* "Voyage de M. E. Simon au Venezuela," Ann. Société entom. de France, vol. lxii. (1893), p. 343.



The left mandible has the outer cutting-edge of four teeth much as in the right, but the accessory appendage is much stouter, thick and dark brown similar to the outer cutting-edge; it ends in several stout teeth, of which the outer one is the longest and strongest, and is followed by two short double teeth; the membranous lobe and the molar tubercle are similar to those of the right mandible.

The *lower lip* consists of two broad lobes somewhat widely separated, with the extremities broadly rounded and thickly covered with short setæ, most of which are directed inwards.

The *first maxillæ* are practically the same in form as those of *Ligia oceanica*, the outer lobe being stout, longer than the inner, and provided at its extremity with about eight strongly-curved setæ, those to the outer side being the longest and stoutest. The inner lobe is more delicate, apparently membranous; its extremity appears concave on its inner side, and it bears the three characteristic plumed setæ, the distal one being very short and the proximal one the longest.

The *second maxillæ* are stoutly formed, oblong in shape, about two and a half times as long as broad, the extremity irregularly rounded, its inner half and the distal portion of the inner margin fringed with setæ; there is also an oblique row of setæ on the surface of the maxilla near the end; the outer margin bears fine setæ towards the base, the more distal portion being apparently free. I can find no trace of the two plumose setæ which are found in *Ligia oceanica* towards the end of the inner margin, and the division into two lobes, which is partially indicated in *Ligia oceanica* and other species, is not recognizable at all in the present species.

The *maxillipedes* also show rather more coalescence of the different parts than those of *Ligia oceanica*; the first joint (*coxa*) is short and very broad, and the exopodite arising from it is short, subtriangular, rounded at the end, and its free margins fringed with setæ; its articulation with the basos is oblique, extending further distally on the anterior (upper) surface than on the posterior, the extremity of the coxa being strongly convex on the anterior surface but straight on the posterior; the next joint (*basos*) is nearly oblong, fully two-thirds as broad as long, its outer margin slightly convex and bearing a fringe of fine setæ; the inner margin is straight, and is bent inwards (i. e. *upwards*, in the usual position of the mouth-parts) to form a piece at right angles to the outer surface of the maxillipedes; this is thickly covered with short fine setæ, and narrows distally where it extends on to the masticatory lobe, which is formed by a prolongation of the inner part of the basos; the masticatory lobe is truncate distally, and bears there two stout teeth and many finer setæ. The terminal portion of the endopodite ("palp") shows indications of being formed of five segments, of which only the first and last are completely separated from the others, the second, third, and fourth being coalesced into a flat plate with the lines of suture visible towards the inner side only; on the outer side the extremity of each joint is marked by one or two stout setæ, the rounded inner margins of the last four segments are thickly covered with short setæ. Fig. *m.xp.*\* shows the maxilliped from its anterior aspect, i. e. that next to the second maxilla, and from this point of view the connection of the masticatory lobe with the basos can be clearly made out; when seen from the posterior (fig. *m.xp.*) the junction of the basos with the

succeeding joint extends right across to the inner margin and makes the masticatory lobe appear separated from the basos though it is directly continuous with it on the anterior surface.

The *first pair of legs* differ considerably in the two sexes. In the female (Pl. 11. fig. 1 p.<sup>1</sup> ♀) the appendage is similar to the succeeding pairs, though rather shorter; the basos is somewhat oblong, and bears a few stout setæ on its upper or inner side at the distal end; the lower or outer surface has a slightly hollowed depression, into which the more distal joints of the limb rest when they are bent back upon the basos, as they are in the usual position of the legs. The shape of the other joints and the arrangement of the setæ on them can be readily made out from the figure: the propodos is cylindrical, much narrower than the carpus, and has on its inner margin a regular row of about six short setæ; the dactylus is somewhat slender, and has the basal portion covered, especially on the outer side, with short fine setæ and a few spiniform ones; the terminal portion forms a strong, curved nail with margins regularly curved and without setæ; the accessory nail is about half as long as the terminal one and much more slender; at the base of the terminal nail arises from the outer margin a long, well-marked seta about as long as the terminal nail, but usually curved backwards and having a slight club-like swelling towards its extremity. These points, with regard to the dactylus, are represented in Pl. 11. fig. 1 p.<sup>7</sup> ♀\*, which shows the extremity of the seventh pair of legs, but with very slight modification the figure and description apply to all the pairs.

In the male the first pair of legs is much stouter than in the female, the meros is larger and more triangular, while the carpus is ovoid, being much expanded on the inner side, and against it the propodos and dactylus closely impinge and form a powerful subchelate hand; the propodos is stout and slightly curved, and the dactylus rather stouter and shorter than in the female. The general appearance of this appendage in the male is very like that of one of the gnathopoda of an amphipod, or like the first pair of legs in *Phreatoicus*, but in these the subchelate hand is formed by the dactylus impinging against the enlarged and swollen propodos, while in the present species the propodos and dactylus together impinge against the enlarged carpus.

The *second pair of legs* in the female is quite similar in form and size to the first. In the male it has the form of a subchelate hand like the first pair, but the carpus is much narrower and its inner edge, which forms the palm, is not so convex.

The *third pair of legs* in the female is quite similar to the preceding pairs in form, but is usually a trifle longer; in the male it may have the carpus very slightly expanded, as in the first and second pairs, but more generally it has nothing of the gnathopod form and is almost identical with the corresponding appendages of the female.

The succeeding pairs of legs in both sexes are gressorial and similar to one another in general form, but there is a gradual increase in length and slenderness as we pass to the seventh pair. In all there is the smooth, slightly concave depression on the basos against which the other joints impinge, and the dactylus always bears the characteristic clubbed seta already described, though in spirit specimens this may sometimes be lost, more frequently so in older and larger forms. The *seventh leg* is represented in Pl. 11. fig. 1 p.<sup>7</sup> ♀, and it is scarcely necessary to give a detailed description of it.

The *pleopoda* present the usual features, and all consist of a short basal portion or protopodite, from which spring the endopodite and exopodite; of these the endopodite is entirely branchial and has its margins perfectly free from setæ, while the exopodite appears to be mainly opercular and usually has its margins more or less fringed with plumose setæ. It will be convenient to describe the pleopoda of the female first, and then to point out the special modifications in the male.

The *first pleopod* has the protopodite short and broad, roughly rectangular but narrowing a little externally; on the outer side it bears a small rounded appendage with margins free from setæ, which appears distinct from the rest of the protopodite though not distinctly separated by any suture or articulation. This appendage, which is found on the first and second pleopoda of both sexes, is perhaps to be looked upon as an "epipodite"; it will, at any rate, be convenient to refer to it by this name. The exopodite is suboval in shape and much larger than the endopodite; its margin bears a few irregular plumose setæ.

The *second pleopod* of the female closely resembles the first, but is slightly larger; from the centre of the sternal plate of the segment is a small subtriangular projection, truncate at the extremity; the epipodite is longer, more pointed at the end, and bears numerous finely-plumose setæ.

The *third, fourth, and fifth pleopoda* are all similar in form, but each a little larger than the preceding one. Pl. 11. fig. 1 *plp.*<sup>3</sup>♂ shows the third pleopod of a male specimen, but will serve almost equally well for that of a female; from the centre of the sternal plate of the segment arises an oval projection, which is produced distally to a fine point; there is no trace of the epipodite, but on the inner side the protopodite is produced into a triangular acutely-pointed process the margins of which bear several plumose setæ; the exopodite is much larger than the endopodite, and is distinctly opercular in structure and has the margins regularly fringed with long plumose hairs; the fourth and fifth pleopods are similar, but as we proceed posteriorly the endopodites, being less covered by succeeding appendages, become more strongly chitinized and more abundantly supplied with stellate pigment cells, the fifth one naturally most so, as it is completely exposed.

In the male the first and second pleopoda are specially modified for the purpose of copulation. In the first pair the pleopod itself is not very different from that of the female, though the exopodite is rather larger and the endopodite is more pointed at the apex, but it is closely associated with the external male organ, which no doubt springs from the last segment of the mesosome but is adherent to the protopodite of the pleopod and in dissection always comes away with it; it forms a long, narrow process, slightly narrowed and curved outwards at the end; this is grooved throughout its whole length on the posterior side, and during life is closely pressed against the anterior side of the long process formed by the endopodite of the second pleopod, and with it forms a tube for the passage of the semen.

In the *second pleopod* of the male the protopodite and the exopodite present little modification, but the whole of the endopodite is specially modified; it forms a 2-jointed penial appendage, strongly chitinized throughout, much more so than the male organ proper already described; the first joint is short, lies transversely, and is moved by

powerful muscles; the second is long, semicylindrical, narrowing and curving outwards at the extremity, which bears numerous fine short setæ with points directed away from the apex; the anterior aspect shows a well-marked groove, from the sides of which near the middle numerous setæ project inwards towards the groove and appear to be for the purpose of holding the male organ against this appendage and keeping it firmly in its place; they probably do so by interlocking with similar setæ on the male organ itself, though these cannot be well made out.

The *uropoda* are of the usual form, the basal portion irregularly cylindrical and somewhat twisted so that when detached it is difficult to get it to lie in its natural position; the outer ramus slightly narrower than the inner, but usually nearly or quite as long; it bears two long setæ at the apex, shorter setæ being usually present on the inner branch; surface of base and rami covered with fine short setæ, giving it a roughened appearance.

### Family II. TRICHONISCIDÆ.

This family was established by Sars for *Trichoniscus* and a few other genera that had previously been classed under the Ligiidæ. It is closely related to that family, but may be recognized from it by the fact that the flagellum of the antenna has only a few joints (not more than six or seven); the eggs are small, and contain only a few ocelli (usually three), and the external male organ is single. The animals are usually small and live in damp situations, none of the pleopoda being provided with air-cavities.

Two genera of this family—i. e., *Trichoniscus* and *Haplophthalmus*—are represented in New Zealand.

#### Genus 1. TRICHONISCUS, Brandt. (Pl. 12. figs. 1 & 2, and Pl. 13. fig. 1.)

*Trichoniscus*, Brandt, *Conspectus Crust. Oniscodorum*, p. 12 (*Bull. Soc. Moscou*, vi. p. 174) (1833).

*Philougria*, Bate & Westwood, *Brit. Sess.-eyed Crust.* ii. p. 454 (1868).

*Trichoniscus*, Budde-Lund, *Isopoda Terrestria*, p. 213 (1885).

*Trichoniscus*, Sars, *Crustacea of Norway*, ii. p. 160 (1898).

*Trichoniscus*, Stebbing, *Proc. Zool. Soc. London*, 1900, p. 565 (1900).

*Generic Characters.*—Body more or less oblong, attenuated behind. Cephalon rounded in front, with small though distinct lateral lobes. Side-plates of the three posterior segments of mesosome more prominent than those of the four preceding segments. Metasome abruptly contracted, with the epimeral plates of the two anterior segments not concealed: last segment narrowly truncate at the tip and slightly emarginate on each side. Eye small but distinct, consisting of only three visual elements imbedded in a dark pigment. Antennulæ with the first joint rather large and curved, last joint generally longer than the second. Antennæ everywhere clothed with small appressed spikes; flagellum much shorter than the peduncle and gradually tapering distally. Oral parts considerably prolonged, giving the buccal mass a pronouncedly conical form. Left mandible with two, right with only a single penicil behind the cutting-part. Maxillipeds with the distal joint of the basal part rather large, and forming at the end outside a broad lamellar expansion finely ciliated at the edge; terminal part lanceolate, with the

outer four joints confluent; masticatory lobe nearly as large as the terminal part, and terminating in a narrow, finely-ciliated lash; epignath oblong-linguiform, with a rounded expansion at the base. Legs of moderate size, slightly increasing in length posteriorly; outer joints extremely spinous. Inner plate of first pair of pleopoda in male greatly produced, biarticulate; that of the second pair of different structure in the different species. Uropoda with the basal part rather broad and flattened, both rami terminating in a pencil of delicate hairs. [Sars, *l. c.* pp. 160-161.]

### Key to Species.

1. Dorsal surface and antennæ with distinct though irregular tubercles . . . . . *T. otakensis*.
2. Dorsal surface smooth or nearly so.
  - a. Surface with scattered longish setæ. Animal small (4 mm.) . . . . . *T. phormianus*.
  - b. Surface without scattered setæ. Animal large (7 mm.) . . . . . *T. Thomsoni*.

#### 1. TRICHONISCUS PHORMIANUS, sp. nov. (Pl. 12. fig. 1.)

*Philougria rosea*, Chilton, Trans. N. Z. Inst. xv. p. 149 & p. 73 (in part) (1883) [*not* of Koch].

*Philougria rosea*, Filhol, Mission de l'île Campbell, p. 439 (in part) (1885).

*Philygia rosea*, Thomson & Chilton, Trans. N. Z. Inst. xviii. p. 157 (in part) (1886).

*Specific Description*.—Male not differing markedly from the female in the general shape of the body. Body oblong-oval, about two and a half times as long as broad. Dorsal surface not very convex, smooth, or with a few small granulations and irregularities; cephalon and each segment of the mesosome with a few scattered, rather long, stout setæ, which are irregularly arranged and extend more or less over the whole surface, but are most readily seen at the sides, especially in the anterior segments; on the metasome there are few or none; these setæ readily break off in spirit specimens. Cephalon transversely oval, lateral lobes small, front slightly convex. Segments of the mesosome of the usual form, the last three with the posterior angles recurved and acuminate. Metasome about one-quarter the length of the body, rather narrow; first two segments short, epimeral plates of the next three small and appressed; last segment with the terminal expansion rather broad, the posterior margin straight or slightly convex, and bearing three or four small setæ.

Antennæ a little less than one-third the length of the body, rather slender, with long setæ at the extremities of the second, third, and fourth joints and along the inner margin of the fifth; these may arise from slight prominences, but the inner margin of the fifth joint does not bear the distinct tubercles found in the next species; outer margin of the joint straight, with short fine setæ; flagellum as long as the fifth joint, of four joints (sometimes only three), pencil of hairs at extremity long.

Uropoda long, outer branch more than twice as long as the base, conical, narrowing to apex; inner branch nearly as long, but much narrower throughout and tapering very gradually to the apex; both covered with small appressed setæ and with long setæ at apex.

*Colour* light brown, with irregular marblings of a darker brown.

*Size* about 4 mm.

*Habitat*.—Very common all over Canterbury, frequently found on the dead decaying leaves of the New Zealand flax (*Phormium*), and always in damp situations. Also from Dunedin, Kenepuru, Greymouth.

*Remarks*.—The separation of the New Zealand species of *Trichoniscus* presents considerable difficulty, and it is quite possible that some modification may have to be made in the division I am here adopting, though it is the best I can make with the material now at my command.

The present species was originally confused by me with *T. otakensis*, and both referred to *Philougria rosea*, Koch. Further investigation has shown that I was dealing with two species, and that though each presents considerable resemblances to *Philougria rosea*, Koch, neither can be considered as identical with that species.

The species now under consideration appears to be distinguished from the next species, *T. otakensis*, by the smoother surface of the body, the more slender and smoother antennæ, the presence of stout setæ on the surface, and by the fact that the male and female are approximately of the same general shape.

The stout setæ on the cephalon and mesosome are very characteristic, but they readily fall off in spirit specimens, and confusion may thereby be introduced. Some of my specimens are now so free from all trace of these setæ that I have sometimes been inclined to think that there must be a form destitute of setæ. On the other hand, I have specimens from Kenepuru collected by Mr. MacMahon in which the setæ are still present; they are rather more numerous and shorter than in Canterbury specimens, and the surface is more uneven and tuberculated; it is possible that these specimens will require a separate species to be established for their reception, but in the meantime I prefer to regard them merely as a variety of *T. phormianus*.

The mouth-parts show such a close general resemblance to those of other species of the genus, such as *T. roseus*, that I have not given figures of them. The mandibles and first and second maxillæ present the usual characters; in the maxillipedes the articulation between the coxa and basos is oblique from the external to the internal face like that already described in *Ligia noræ-zealandiæ*; the masticatory lobe into which the basos is prolonged is shorter than the palp, and bears at the end a separate conical portion, thickly covered with fine setæ arranged radially and produced distally into the short terminal lash; in these points this species appears to agree closely with *Trichoniscus Leydigii* as figured and described by Max Weber\*.

The seven pairs of legs present no feature of special importance, and I have not observed that any of them are specially modified in the male. The dactylar seta is long and extends fully to the end of the dactylus; at about the middle of its length it divides into two branches, the outer one the thicker, both further subdividing into numerous very fine hairs.

In the female the first pleopod is very like that of *T. pusillus* figured by Sars, but the

\* *L. c.* p. 616, pl. xxviii. fig. 18.



endopodite is larger in comparison with the exopodite. In the second pleopod the endopodite is narrow and projects considerably beyond the exopodite. In both pairs there is a lateral expansion of the protopodite corresponding to the "epipodite" described in *Ligia novæ-zeelandiæ*. The remaining pleopoda are of the usual form.

In the male the first two pairs of pleopoda are specially modified, as in other species, for sexual purposes, but they differ considerably in detail. The first pleopod, together with the sexual appendage, is shown in figure *plp.*<sup>1</sup> ♂. The sexual appendage is soft and membranous, spatulate in form; the endopodite is narrow, subtriangular, and ends in a very long, narrow, chitinous, styliform process which tapers gradually to the very acute apex. In the second pleopod (fig. *plp.*<sup>2</sup>) the endopodite is modified into a 3-jointed penial appendage, strong and highly chitinised; it is of nearly the same breadth throughout except at the extremity, where it narrows abruptly and ends acutely.

## 2. *TRICHONISCUS OTAKENSIS*, sp. nov. (Pl. 12. fig. 2.)

*Philougria rosea*, Chilton, Trans. N. Z. Inst. xv. p. 149, and p. 73 (in part) (1883).

*Philygria rosea*, Thomson & Chilton, Trans. N. Z. Inst. xviii. p. 157 (in part) (1886).

*Philougria rosea*, Filhol, Mission de l'île Campbell, p. 439 (in part) (1885).

*Specific description*.—Male and female differing in the shape of the body.

*Female*.—Body oblong oval,  $2\frac{1}{2}$  times as long as broad; whole dorsal surface thickly covered with irregular, densely crowded, roughish tubercles. Cephalon with the lateral lobes fairly large; margins with two or three setæ, but hardly denticulate; front slightly convex. Segments of mesosome slightly separated laterally; first four segments with the lateral angles rounded, the last three with the postero-lateral angles recurved and acuminate. Metasome rather less than one-fourth the length of the body; last segment with its posterior margin straight and bearing three or four small setæ.

Antennæ rather stout; fourth joint of peduncle stout; fifth joint narrowed at base and expanding slightly distally, its inner margin with four or five distinct prominences, from which short stout setæ may arise; outer margin straight, fringed with fine setæ; flagellum nearly as long as the last joint of peduncle, composed of four joints. Uropoda rather short, stouter than in *T. phormianus*; outer ramus twice as long as the base.

*Male*.—Much narrower than the female, the greatest breadth less than one-third the length; none of the legs specially modified.

*Colour* light brown, with markings of darker brown.

*Length* about 4 mm.

*Habitat*.—Widely distributed throughout the South Island, N. Z., in damp situations.

*Remarks*.—This species closely resembles the preceding one in most respects, but can be readily distinguished from it by the tuberculated surface, the stouter antennæ and uropoda, and, in the male, by the narrow form of the body.

The mouth-parts, legs, and pleopoda (including those specially modified in the male) closely resemble those of *T. phormianus* and do not call for special description.

I have a few specimens from Greymouth, collected by Mr. R. Helms, that I refer to this species with some hesitation. The specimens, which appear to be all females, are of slightly larger size, and have the body broader and more compact than in the typical

forms; the tubercles both on the body and on the antennæ are particularly well marked, and, in some specimens at any rate, the flagellum of the antennæ contains five joints.

3. *TRICHONISCUS THOMSONI*, Chilton. (Pl. 13. fig. 1.)

*Philygia Thomsoni*, Chilton, Trans. N. Z. Inst. xviii. p. 159, pl. v. figs. 1-6 (1886).

*Specific description*.—Oblong oval, greatest breadth fully half the length, fairly convex, surface quite smooth. Cephalon short, transverse, more than twice as broad as long; lateral lobes small, not visible in dorsal view, front slightly convex, a slight transverse depression a little anterior to the eyes, and an oblique depression starting near the median line between the eyes and extending backwards and outwards. Epimera largely developed, those of the first segment of mesosome produced anteriorly into rounded lobes enclosing fully one-half of the cephalon, those of the second and third segments with the posterior angles reetangular, those of the fourth to seventh segments recurved and acuminate in progressive degree, those of the seventh reaching as far back as the posterior border of the fourth segment of metasome. Metasome much narrower than last segment of mesosome; third, fourth and fifth segments with fairly-developed but closely-appressed epimera; last segment with posterior border straight and bearing three or four small setæ.

Antennæ slender, fourth joint of peduncle nearly as long as the fifth and slightly broader, all covered with fine setæ; one or two longer ones at the extremities of the second, third and fourth joints; flagellum about as long as the last joint of peduncle, of at least five joints; articulations between the more distal joints very indistinct. Legs rather long, increasing considerably in length posteriorly, very spiny. Dactylar seta large and well developed, dividing into two branches, each of which subdivides in many fine hairs. Uropoda rather long, about two-thirds the length of metasome; outer ramus much the stouter, elongate, conical in outline; inner three-fourths the length of the outer, cylindrical, tapering very gradually, both ending in a few setæ.

*Colour* a light brown, with the greater part of the body covered with markings of a much darker brown, sometimes nearly black; legs with irregular alternate markings of light and dark brown.

*Length* about 7 mm.

*Habitat*.—Widely distributed over the whole of the South Island.

*Remarks*.—This species can usually be recognised by the wide body with greatly developed epimera, by the smooth, almost shining appearance of the dorsal surface, and by the five joints in the flagellum of the antenna. In smaller specimens, however, the epimera are not so much expanded, and the articulation in the flagellum may be very indistinct and identification is the more difficult. Though a true *Trichoniscus* in the mouth-parts, metasome, &c., the general outline is more suggestive of an *Oniscus* or *Porcellis*.

The mouth-parts closely resemble those of the preceding species. The pleopoda also are very similar, except that in the second pleopod the endopodite is more elongate in the female, and in the male the penial appendage formed by it is of a slightly different shape.

## Genus 2. HAPLOPHTHALMUS, Schöbl. (1860).

*Haplophthalmus*, Sars, Crustacea of Norway, ii. p. 166 (1899).

*Generic characters*.—"Body oblong, moderately convex, sculptured dorsally with more or less distinct longitudinal ribs. Cephalon with the front triangularly produced, though scarcely defined from the epistome; lateral lobes rather large. Side plates of mesosome lamellarly expanded, discontiguous. Metasome not abruptly contracted, epimeral plates of the two anterior segments small, those of the three succeeding ones well developed, laminar; last segment of a similar shape to that in the two preceding genera [*Trichoniscus* and *Trichoniscoides*]. Eyes very small, simple, subdorsal. Antennulæ and antennæ much as in *Trichoniscus*. Oral parts likewise rather similar, except that the terminal part of the maxillipedes is obscurely 5-articulate, and the epignath simple, lanceolate. Legs short and thick, scarcely at all increasing in length posteriorly. First pair of pleopoda in female very small and rudimentary; those in the male well developed, with the inner ramus strongly produced, biarticulate, terminal joint spiniform; inner ramus of second pair in male likewise produced, triarticulate, last joint narrow, styliform. Uropoda with the inner ramus originating inside a broad expansion of the basal part, and terminating, as in the genus *Trichoniscoides*, in a single slender spine." [Sars, *l.c.* p. 166.]

The genus is represented in New Zealand by the following species only:—

## 1. HAPLOPHTHALMUS HELMSII, sp. nov. (Plate 12, fig. 3.)

*Specific description*.—Oblong-oval, about twice as long as broad; strongly convex, the central portion being raised somewhat abruptly above the epimeral portions; epimera well developed and somewhat widely separated. Cephalon with the lateral lobes large; on the dorsal surface between the eyes are two rather large, rounded, roughened tubercles; surface in front of these sloping, rough and uneven: front bluntly triangular. All the segments of the mesosome bear at the outer border of the central portion a raised rounded ridge; posteriorly this becomes more marked, and on the seventh segment the ridges end in two well-marked tubercles projecting backwards a little over the metasome; on the fourth anterior segments of the mesosome there is on each side a smaller and less-marked ridge internal to the one already described and parallel to it. Metasome rather small, not quite one-fourth the length of the body; first three segments short and without epimeral expansions, fourth and fifth segments longer and with well-developed epimera; last segment very short, more than twice as broad as long, posterior border straight. Surface of metasome rough like that of the whole body but without distinct ridges or tubercles.

Antennæ short, not quite one-fourth the length of the body, rather stout; fourth segment of peduncle a little expanded, shorter than the fifth, which is narrowed at base, all with appressed scales and a few short setæ, one or two longer setæ on the fifth joint; flagellum as long as the fourth joint of peduncle, of three joints, ending in a pencil of long hairs.

Legs of the usual character, short and rather stout, not visible in dorsal view; dactylar

seta apparently similar to that found in *Trichoniscus*. Uropoda very short, base large and broad, rami short, inner one the more slender, arising anteriorly to the outer, but reaching nearly as far posteriorly.

*Colour* brown.

*Length* 4 mm.

*Habitat*.—Greymouth, a single specimen collected by R. Helms.

*Remarks*.—I have only the one specimen of this species and am therefore unable to describe the mouth-parts, pleopoda, &c. In most respects it agrees well with the generic characters, but differs in having the first *three* (instead of *two*) segments of the metasome small and without lateral expansions.

### Family III. TYLIDÆ.

This family agrees with the *Ligiidæ* and the *Trichoniscidæ* in having a well-developed molar tubercle on the mandibles and three plumose bristles on the inner lobe of the first maxilla. The terminal portion of the maxillipedes is also of fair size, longer than the masticatory lobe. It differs markedly in having the uropoda short and entirely concealed beneath the terminal segment. The pleopoda, too, are of a special structure, and the epimera of the second to seventh segments of the mesome are quite distinct from their segments. The body is convex and the animal capable of rolling into a ball. The metasome consists of six separate segments.

The family contains the single genus *Tylos*, of which numerous species have been described, chiefly from tropical and subtropical regions.

### Genus 1. TYLOS, Latreille.

*Tylos*, Latreille, Règne Animal, iv. p. 141 (1829).

As this is the only genus, it may be considered as having the same characters as the family.

#### 1. TYLOS NEOZELANICUS, sp. nov. (Plate 13. fig. 2.)

*Specific characters*.—Body oval, very convex, rather more than half as broad as long, surface minutely granular and with minute setæ which are most evident at the margins. Lateral margin of the cephalon below the eyes produced downwards into a truncated and slightly emarginate process with raised border, the basal joint of the antennæ fitting into a hollow between this and the frontal margin. Anterior margin straight, slightly raised.

First segment of mesosome with the side-plate large, expanding laterally, not marked off from central portion, its front margin fitting closely against the cephalon below the eyes and produced anteriorly into a rounded lobe; inferior margin with a shallow sulcus; next three segments with side-plates subquadrate, with inferior angles rounded; side-plates of last three segments similar in shape, but larger, and increasing in size posteriorly; all clearly marked off from their segments. Last segment of metasome

quadrangular; surface convex and a little uneven, with depressed line parallel to hinder margin; posterior margin slightly convex and fitting evenly into the space between the rather small side-plates of the fifth segment.

Eyes rather large, convex, with about 40 ocelli. Antennulæ apparently 1-jointed and immobile. Antennæ reaching to posterior border of the first segment of mesosome, last joint of peduncle about twice as long as the fourth and as long as the flagellum; first joint of flagellum strongly geniculate with the peduncle, of the same length as the second, third rather longer, fourth very small, almost rudimentary; the whole antennæ covered with numerous short, bluntish setæ.

First pair of legs with anterior margin of the basos produced near the distal end into a triangular process, and with a shallow groove posterior to this for the reception of the distal portion of the limb when bent back; second pair with similar but less marked structure; legs scarcely increasing in length posteriorly, all very setose, the setæ on the posterior pairs larger and stouter than on the anterior pairs.

Fifth pleopoda with the exopodites strongly chitinised, large, trapezoidal, articulated at the postero-lateral angles, and projecting inwards and forwards so as to meet in the median line and cover a large portion of the anterior pleopoda. Uropoda triangular, outer side convex and with a few setæ, inner margin straight, fringed with fine setæ, terminal joint small, bearing a few fine setæ.

*Colour*.—Whitish or light yellow, with scattered black spots and usually with opaque white or silvery spots arranged more or less closely in patches; some of the specimens darker, especially along median line.

*Length*.—About 14 mm.

*Habitat*.—Lyal's Bay, Wellington (*R. M. Laing*), "Wellington, under tussocks near the beach" (*G. M. Thomson*).

*Remarks*.—I have some hesitation in describing this as a new species, for all the species of the genus appear to be very similar in general appearance and to be distinguished chiefly by differences in the front of the cephalon and the pleopoda, which are somewhat difficult to describe accurately. It is probably not very different from *Tylos spinulosus*, Dana, from Tierra del Fuego, but appears to be less spiny and to differ in the antennæ, for Dana describes and draws the flagellum as "3-jointed, the first joint but little shorter than the preceding, and the second as long as the following."

#### Family IV. SCYPHACIDÆ.

*Scyphacinæ*, Dana (in part), U. S. Explor. Exped., Crust. ii. p. 716 (1853).

Mandibles without molar tubercle, its place being taken by a tuft of long stiff setæ or bristles; inner lobe of first maxilla with two plumose bristles; maxillipedes with the terminal joints fairly well developed, lamellar, longer than the masticatory lobe; external male organ single.

The family, for which I propose the definition just given, corresponds in part with Dana's subfamily *Scyphacinæ*, for he rightly observed that in the maxillipedes, *Scyphax* differs considerably from the *Oniscidæ*, though his description that they are 2-jointed is,

perhaps, a little misleading. In making it he appears to have counted the basos as one joint and all the terminal part as the second. He did not reckon in the coxa, which is usually more or less distinct, and he included the ischium, which is also usually distinct, with the terminal portion which generally shows indications that it is composed of three or four joints. In cases of this kind the actual number of joints is less important than the comparative sizes of those that are represented, though of course it is not easy to express this in brief language.

I include under this family the genera *Scyphax*, Dana, *Actæcia*, Dana, and *Scyphoniscus*, gen. nov., all of which are represented in New Zealand. It will, I think, also include *Scyphacella*, S. I. Smith, and *Actoniscus*, Hayer, both of which are discussed in another part of this paper, and *Philougria marina*, Chilton, which Stebbing has rightly said cannot remain under *Philougria*, probably also belongs to this family, though as yet I have not had time to examine it sufficiently to say whether it can be referred to any of the genera mentioned or not.

It may be worth while to point out that Kinahan, in his excellent "Analysis of Certain Allied Genera of Terrestrial Isopoda," published in 1857, appears to have recognised the fact that *Scyphax* and *Actæcia* probably formed types of separate families, though owing to the great difference between them in general appearance, he evidently did not think of placing them both in the same family\*. The three genera that I have included in this family all agree pretty closely in the mouth-parts and pleopoda, and I am inclined to attach comparatively little importance to the external form of the body.

#### Genus 1. SCYPHAX, Dana.

*Scyphax*, Dana, U. S. Explor. Exped., Crust. ii. p. 733 (1853).

*Scyphax*, Miers, Cat. New Zealand Crust. p. 101 (1876).

*Scyphax*, Budde-Lund, Isopoda Terrestria, p. 231 (1885).

*Generic description*.—Body somewhat convex, not capable of rolling into a ball; epimera moderately developed. Metasome not abruptly contracted, last segment not much produced. Eyes large, of very many ocelli, crescent-shaped, occupying the sides of the cephalon. Antennæ with the flagellum 3- or 4-jointed. Second maxilla with the outer margin a little angularly produced near the base. Mandibles with few penicils behind the cutting part. Legs increasing in length posteriorly. Opercular plates of pleopoda without any air-cavities. Uropoda exposed, inner branch arising only slightly in front of the outer.

*Remarks*.—I have ventured to give a new diagnosis for this genus which was established many years ago by Dana for the single species *S. ornatus*. In 1876, Miers added a new species, *S. intermedius*, but this, as shown below, proves to be the same as *S. ornatus*.

Another species, *S. setiger*, from New Caledonia, was added in 1885 by Budde-Lund, who gave a diagnosis of the genus based mainly on external characters, and considered

\* Natural History Review, iv. Proceedings of Societies, pp. 274 & 275 (1857).



it merely a subgenus of *Oniscus*. In 1874 a genus, *Scyphacella*, was established by S. I. Smith\*, who says:—"This genus differs from *Scyphax* most notably in the form of the maxillipedes, which in *Scyphax* have the terminal segment broad and serrately lobed, while in our genus it is elongated, tapering, and has entire margins. In *Scyphax* also the posterior pair of legs are much smaller than the others, and weak; the last segment of the abdomen is truncated at the apex, and the articulations between the segments of the terminal portion of the antennæ are much more complete than in our species. The general form and appearance of the genera are the same, and the known species agree remarkably in habits. . . ." Budde-Lund† gives Smith's species, *Scyphacella arenicola*, as nearly related to *Trichoniscus albidus*; and Sars‡, following Budde-Lund, refers to the genus *Scyphacella* as coming under his family Trichoniscidæ. It appears, however, from Smith's remarks that his genus is really nearer to *Scyphax* even than he thought, for of the four points of difference which he gives, two are based on errors in Dana's description, for the seventh pair of legs in *Scyphax* are small and weak only in immature forms and the terminal segment is not truncate, the mistake here having arisen from the fact that the lateral margins of the terminal segment are not shown in his figure. In the other two points of difference *Scyphacella* certainly does approach *Trichoniscus*, but they are, I think, only of comparatively little importance, and the spiny antennæ and whole general appearance of *Scyphacella* are more like *Scyphax* than any *Trichoniscus* that I know of. It is, moreover, evident that *Scyphacella* cannot come under the Trichoniscidæ as defined by Sars, for (1) the metasome is not much narrower than the mesosome, and (2) the eyes, instead of being "small or wholly wanting," are large and prominent. Of course the question could be settled at once if we knew whether the mandible in *Scyphacella* has a molar tubercle or not, and whether the inner lobe of the maxilla has three or two plumose bristles. Unfortunately, no special information is given on these points, either by Smith or by Hayer, who afterwards examined the species. But the mandibles of *Scyphax* are figured by Dana, and presumably these drawings would be noted by Smith, who evidently examined those of *Scyphacella*, for he says "mandibles slender," and if these had possessed a molar tubercle he would almost certainly have noticed it.

Until the question can be settled by the examination of specimens, I think we are justified in including *Scyphacella* under the Scyphacidæ as nearly allied to *Scyphax* if not actually identical therewith.

The genus *Scyphax* is represented in New Zealand only by one species, though another is occasionally classed under it.

# 1. SCYPHAX ORNATUS, Dana (1853). (Plate 14. fig. 2, and Plate 15. fig. 1.)

*Scyphax ornatus*, Dana, U. S. Explor. Exped., Crust. ii. p. 734, pl. xlviii. fig. 5 (1853).

*Scyphax ornatus*, Miers, Cat. N. Z. Crust. p. 101 (1876).

*Scyphax intermedius*, Miers, Annals & Mag. Nat. Hist. ser. 4, xvii. p. 227 (1876); Cat. N. Z. Crust. p. 102, pl. ii. fig. 8 (1876).

\* Rep. U. S. Fisheries, pt. i. p. 567 (1874).

† L. c. p. 249.

‡ L. c. p. 160.

*Scyphax ornatus*, Thomson & Chilton, Trans. N. Z. Inst. xviii. p. 158 (1886).

*Scyphax ornatus*, Budde-Lund, Isopoda Terrestria, p. 233 (1885).

*Scyphax intermedius*, Budde-Lund, Isopoda Terrestria, p. 233 (1885).

? *Philoscia violacea*, Filhol, Mission de l'île Campbell, Crust. p. 445, pl. liv. fig. 5 (1885).

*Scyphax ornatus*, Filhol, l. c. p. 443 (1885).

*Scyphax intermedius*, Filhol, l. c. p. 444 (1885).

*Scyphax intermedius*, Thomson & Chilton, Trans. N. Z. Inst. xviii. p. 158 (1886).

*Specific description*.—Body elliptical, fairly convex, breadth about half the length, surface finely granular, in smaller specimens sometimes rough with minute setæ. Surface of cephalon flat, depressed. Metasome not abruptly narrower than mesosome, epimeræ of third to fifth segments of moderate size, last segment triangular, much broader than long, sides concave, extremity bluntly pointed, bearing a few short setæ and with a slight depression on its upper surface.

Eyes very large, crescent-shaped, occupying the whole lateral margins of the cephalon and nearly meeting in front; ocelli very numerous, about 150 to 200, arranged in four longitudinal rows. Antennæ about half the length of the body, spiny in small specimens, in large ones with granulations or small tubercles in addition to the small spines; flagellum as long as the fifth joint of peduncle, which is considerably longer than the fourth, consisting of three joints, the third being followed by a minute terminal joint ending in a tuft of short setæ, first joint longer than the second and slightly shorter than the third. Anterior pairs of legs shorter and stouter than the posterior pairs, which are rather long, the seventh pair not fully developed till animal is nearly adult. Uropoda with the base large, extending a little beyond the extremity of the terminal segment, lateral border with a distinct keel, rami rather narrow, cylindrical, spinose, the inner one very slightly shorter than the outer and not arising much in front of it.

*Colour* variegated, irregularly spotted with yellowish red, grey, brownish red or black.

*Length* of largest specimens about 18 mm.

*Habitat*.—On sandy shores in the North Island and also from Westport. Not found in the south of South Island.

*Remarks*.—This species was described and figured by Dana in 1853, but does not appear to have been recognised since. Miers described his *Scyphax intermedius* as a separate species in 1876, being misled by Dana's figure of the whole animal where the margins of the terminal segment of the metasome are not marked and the segment consequently appears much more broadly truncate than it really is. I have seen Miers's type specimen in the British Museum and have no doubt that it is only a large specimen of *S. ornatus*, Dana. Although Filhol's description and figures are not altogether satisfactory, I have little doubt that his *Philoscia violacea* also belongs to this species; the large crescentic eyes clearly show that the species cannot be placed under *Philoscia*. In 1885 Budde-Lund described a species, *Scyphax setiger*, from New Caledonia which probably will come near to *S. ornatus*, Dana, though the eyes seem to contain fewer ocelli and the proportions of the joints of the flagellum of the antennæ are different.

Although Dana was undoubtedly dealing with immature specimens when he described

the seventh pair of legs as "much smaller than the others, weak," it is nevertheless true that in this species the development of these legs appears to be delayed longer than is usually the case. In specimens of from 4 to 5 mm. in length, which are running actively on the beach and not otherwise immature, the seventh segment of the mesosome is small and the seventh pair of legs represented either by a small bud or by a weak, non-chitinated appendage, with the joints only faintly indicated and surface free from setæ; in specimens a little larger (6 mm.) the seventh segment is more developed, but still smaller than the sixth, and the legs are of the usual shape but smaller than the sixth and less abundantly supplied with setæ. In specimens of 9 mm. in length I found the seventh segment and appendages fully developed; the male organs were also present, and the specimens apparently fully adult.

Most of the more important points in the appendages of this species have been referred to in the discussion of the genus already given. I give here a few additional notes.

The mandibles are of the type usual in the family. The outer cutting-edge in the right contains three or four stout teeth, brown in colour and highly chitinated; the inner cutting-edge is more transparent, slender, and ends in two large teeth and one or two smaller ones; it is followed by a membranous lappet, the sides and margin of which are densely setose; between this and the dense tuft of stiff plumose bristles is a single large plumose seta. The left mandible is very similar, but the inner cutting-edge is much larger and stouter, and ends in three large teeth which are brown in colour and as strongly chitinated as those of the outer cutting-edge, and there are two plumose setæ between the membranous lappet and the tuft of setæ representing the molar tubercle.

The first maxilla is of the usual form: in the second the external lobe at the end is very small, and the outer margin shows a prominence near the base like that drawn and described by Sars in *Oniscus* and some allied genera.

In the maxillipede the exopodite is about half as long as the basos, oblong with the end rounded; the outer margin of the basos is somewhat expanded, and is fringed with fine setæ towards the distal end; the masticatory lobe is about half as long as the terminal portion of the maxillipede, and has the end obliquely truncate and fringed with setæ; the ischium is short, distinctly separated from adjacent points; on the outer aspect of both the basos and ischium are three or four short setæ near the distal margin; the four terminal joints are coalesced into a single lamelliform plate, with four distinct lobes on inner side representing the different joints of which it is composed.

The legs of the mesosome are spiny, the anterior pairs shorter and stouter than the posterior; the dactylus is long, and has its basal part thickly covered with short setæ, the terminal claw long, narrow and slightly curved, secondary claw very narrow, almost like an ordinary seta. There is no special "dactylar seta."

In the male the first pleopod is remarkable in having the exopodite very large and operculiform; it is articulated as usual to the lateral part of the prolopodite, and extends anteriorly and posteriorly into two large rounded lobes, which show branching thicken-

ings apparently intended to strengthen the large flat plate thus formed; the endopodite consists of a single long slender appendage, gradually narrowing to the end; the epipodite is formed of an oblong lobe with rounded end. The external male organ is short, rather narrow and rounded at the end.

The second pleopod of the male has the exopodite of fair size, subquadrate with angles rounded off, and of similar structure to that of the first pleopod; the endopodite is represented by a 2-jointed appendage, the first joint extending directly inwards like a prolongation of the base, the second at right angles to this, as long as the exopodite, gradually tapering to an acute apex.

The succeeding pleopoda have the exopodite much larger than the endopodite, and apparently mainly opercular; the endopodite is subtriangular, with the inner portion thickened, and is branchial in function.

The uropoda have been already sufficiently described.

2. *SCYPHAX* (?) *AUCKLANDIÆ*, G. M. Thomson. (Plate 15. fig. 2.)

*Actæcia aucklandiæ*, G. M. Thomson, Trans. N. Z. Inst. xi. p. 249 (1879).

*Actæcia aucklandiæ*, Budde-Lund, Isopoda Terrestria, p. 239 (1885).

*Actæcia aucklandiæ*, Filhol, Mission de l'île Campbell, p. 443 (1885).

? *Oniscus novæ-zealandiæ*, Filhol, l. c. p. 441, Pl. liv. fig. 7 (1885).

*Actæcia aucklandiæ*, Thomson & Chilton, Trans. N. Z. Inst. xviii. p. 158 (1886).

*Specific description*.—Body oblong-oval, length about twice the greatest breadth, sides of mesosome parallel. Cephalon with lateral lobes large and broad; front triangular, depressed, somewhat excavate in the middle (in dorsal vein appearing nearly straight); an oblique ridge on each side running backwards and outwards behind the eyes from near the centre in front to the posterior margin of the cephalon; surface between these ridges roughly tubercular. Side-plates of mesosome well developed, especially those of the first segment; posterior margin of first segment slightly sinuous, posterior angles subacute, posterior angles of succeeding segments becoming more and more acute.

On each segment is a small oblique ridge on the side-plate running backwards and outwards, and between these ridges each segment bears numerous irregular tubercles, some rounded, others more acute; on the three anterior segments they are rather less marked and irregularly arranged; on the four posterior segments they form a regular row of somewhat pointed tubercles projecting a little backward along the posterior margin of the segment, with irregular granulations anterior to this row.

Metasome not abruptly narrower than mesosome, first two segments short, their sides overlapped by the last segment of mesosome; side-plates of third to fifth segments large, produced acutely backwards; surface of each of these segments with a transverse row of small tubercles, and with others irregularly distributed; terminal segment short, much broader than long, triangular, sides concave, extremity rounded and depressed, fitting closely on to the bases of the uropoda.

Eyes of moderate size, situated on a slight prominence above the lateral lobes, and external to the oblique ridges. Antennules easily visible. Antennæ short, reaching backwards to the posterior border of the second segment of mesosome; first three joints short, subequal; fourth longer, somewhat broadened; fifth a little longer than the

fourth, slightly sinuous, narrowed at base; flagellum as long as the fourth joint, stout, composed of four joints, the first two short, subequal, third longer, fourth very short, articulations not very distinct; whole antenna roughly granular, with very few setæ. Legs rather short, not visible in dorsal view, and not increasing in length posteriorly.

Pleopoda apparently as in *Oniscus*, opercular plates with outer margin incurved but not so abruptly notched as in *Oniscus*; no air-cavities. Uropoda with the base large and meeting in the median line, lateral portion expanded, flattened and keeled externally, ending acutely external to the outer ramus; both rami exposed, inner ramus arising a little anteriorly to the outer, but extending backwards to the same point, but with apex rounded and with a very few minute setæ.

*Colour* brown.

*Length* 20 mm., breadth 9 mm.

*Habitat*.—Auckland Island (*Mr. Jennings*).

*Remarks*.—The above description is taken from a female, the only specimen I have seen. According to Mr. Thomson the male has the whole surface of the body nearly smooth.

I refer Filhol's *Oniscus novæ-zealandiæ* to this species with considerable doubt, for his description and figure are hardly sufficient to permit of certain identification. However, some points in his description as to the antennæ and uropoda, and especially that of the tubercles—"les granulations de la rangée postérieure sont plus détachées et leur sommet un peu aigu est dirigé en arrière"—apply exactly to the species in question. He states that his specimens were obtained near Wellington.

I have placed the species under *Scyphax* only provisionally, for I have had only one specimen and have not been able to examine all the mouth-parts, &c. It can hardly come under *Actæcia*, in which it was placed by Mr. Thomson, and though it has considerable resemblance to *Oniscus*, it differs markedly from that genus in the antennæ and uropoda, and also in the maxillipedes, for these, as shown in fig. 2 *mxp.*, have the terminal part well developed, much longer than the masticatory lobe, and with clear indications of the joints of which it is composed. In this, and in the maxillæ which I have also been able to examine, the species resembles *Scyphax*, and I think it will certainly come under the same family, but it differs greatly from *Scyphax* in the cephalon and in the much smaller eyes. It probably lives on the sea-shore like the rest of the *Scyphacidae*.

## Genus 2. SCYPHONISCUS (novum).

*Generic Characters*.—Body rather narrow, lateral parts not greatly developed. Cephalon with large broad lateral lobes. Metasome abruptly contracted, first two segments rather short, third to fifth with small epimera, last segment short, triangular. Eyes of moderate size, sublateral. Antennule of three joints, the last small, but bearing two or three sensory setæ. Antennæ with the flagellum of three ill-defined joints. Mandibles with a membranous hairy lappet behind the two dentate lamellæ, followed by a long recurved brush-like seta: molar process represented by a dense tuft of recurved setæ of unequal length. Anterior maxillæ with the outer lobe rather weak, some dentate

setæ on its inner margin near the apex, end with a dense row of simple hair-like setæ; inner lobe small, delicate, with two hairy bristles. Second maxillæ distinctly bilobed at the extremity, outer edge not angularly produced near the base. Maxillipedes with the basos rather narrow; masticatory lobe well developed, rounded at end, terminal portion of fair size with the last four joints coalesced into a single triangular plate. Legs short, not increasing much in length posteriorly. Pleopoda simple, opercular plates delicate, and none of them with air-cavities. Uropoda rather produced, base only partially covered by terminal segment, rami not flattened.

*Remarks.*—In general appearance this genus at first recalls *Trichoniscus*. The most important character by which it is separated from other genera appears to be the structure of the first maxilla, the outer lobe of which is very peculiar, and quite different from that of any other Terrestrial Isopod that I am acquainted with.\* In the mandibles with the dense tuft of stiff setæ apparently representing the molar tubercle and in the maxillipedes this genus seems to resemble somewhat closely *Scyphar ornatus*, and the two species of *Actæcia* described in this paper. The type species, which is the only one at present known, was found on the sea-beach within reach of high tides, and I at first thought that the *Philougria marina* described by me in 1885 † would belong to the same genus, but I find that it has the first maxillæ normal, though, as Stebbing has recently pointed out, the species cannot for other reasons come under *Trichoniscus*‡, and probably will be found to belong to the Scyphacidae.

*SCYPHONISCUS WAITATENSIS*, sp. nov. (Plate 14. fig. 1.)

*Specific description.*—Body narrow oval, rather more than twice as long as broad; surface of cephalon and mesosome with small rounded tubercles and other irregularities, generally forming a somewhat irregular transverse row near the hinder edge of each segment. Cephalon with the broad lateral lobes not very clearly defined at their bases, front triangularly produced. Posterior margins of the first four segments of mesosome straight, those of last three with the posterior angles more and more recurved posteriorly. Metasome with the first segment short, second longer, third to fifth with moderate appressed epimera; last segment short, about twice as broad as long, triangular, ending in a slightly rounded angle, sides concave.

Antennæ with the fifth joint of peduncle much longer than the fourth, flagellum as long as the fourth joint, of three joints, the first short, second twice as long, third narrow, about as long as the first, whole antennæ covered with short stout setæ. Legs short, dactyla stout, with the secondary nail small or obsolete; dactylar seta arising near the base of dactylus, longer than dactylus, 2-branched, the outer the stouter and plumose, inner one apparently simple.

*Colour* brown.

\* Dollfus has drawn attention to some abnormalities in the mouth-parts of *Mesarmadillo Alluandi*, Dollfus, the most striking being that the inner lobe of the first maxillæ bears nine hairy bristles, instead of the two usually present in *Armadillidium* (Annales de la Société Entom. de France (1892), lxi, p. 386).

† Proc. Linn. Soc. N.S.W., ix, part 3, p. 463.

‡ Proc. Zool. Soc. London, 1900, p. 565.



*Length of largest specimen seen 3.5 mm.*

*Habitat.*—Blueskin Bay, Otago, under seaweed, &c. at high-water mark.

*Remarks.*—Of this species I have only a few small specimens collected at Blueskin Bay about 1887. I have never found it since, though I have frequently searched the same locality and other similar situations, and I am unable to say whether it attains a larger size or not. In order that its affinities may be made as clear as possible, I have figured the mouth-parts in some detail, and add further description of some of its appendages.

The upper lip is of the usual structure.

The *left mandible* has the outer cutting-edge formed of three well-marked teeth, strongly chitinated, the inner cutting-edge similar and of four teeth; near its base arises a hairy membranaceous lappet with the innermost seta longer than the others; next, at a considerable distance, follows a single long-curved, feathered seta; and next, from a slight prominence, a brush-like tuft of stiff simple setæ, the outer ones the shortest, the others gradually increasing in length, the innermost ones being very long.

The *right mandible* is similar, but the outer cutting-edge appears to bear four teeth, and the inner cutting-edge is smaller, less chitinous, and ends in three or four small sharp teeth, apparently arranged in a circle round the extremity.

Lower lip formed of two rounded lobes with numerous setæ directed inwards, and between them a narrow tongue-like process with its margins thickly fringed with setæ.

The *first maxillæ* has the outer lobe oblong in shape, its inner margin fringed in distal half with fine setæ, and towards the end bearing about ten dentate setæ of various sizes and irregularly arranged; the extremity and a little of the outer margin bears a compact row of long, simple, hair-like setæ, the outer ones being the longest, the inner ones stouter and a little incurved. Inner lobe of normal form, the distal plumose bristle much shorter than the other.

The *second maxillæ* form a delicate oblong plate, distinctly cleft at the apex, outer lobe about half as large as the inner, both rounded and bearing delicate setæ, the inner one with a row of short stouter setæ also.

The *maxillipedes* have the epipodite narrow oblong, as long as the basos, truncate at end, end and distal half of outer margin with delicate setæ; basos narrow, its outer margin not expanded; masticatory lobe large, more than half the length of the palp; palp with the ischium distinct, but the remaining joints combined into a triangular plate with its inner margin thickly fringed with setæ, and with a faint indication of lobes indicating the separate joints.

The first and seventh legs are shown in the plate, and do not require further description; the dactylar seta is large and well marked; its general appearance will be best learnt from the figure.

The pleopoda appear to be all of about the same structure; in the first the endopodite is of nearly the same size as the exopodite, but narrower; there is a small "epipodite" arising from the basal portion. In the third and succeeding pleopoda the endopodite arises considerably more proximally than the exopodite, and is smaller in proportion. I have not been able to examine the pleopoda in the male. The uropoda have already been sufficiently described.

Genus 3. *ACTÆCIA*, Dana, 1853.

*Actæcia*, Dana, U. S. Explor. Exped., Crust. ii. p. 734 (1853).

*Actæcia*, G. M. Thomson, Trans. N. Z. Inst. xi. p. 249 (1879).

*Cylloma*, Budde-Lund, Isopoda Terrestria, p. 46 (1885).

*Actæcia*, G. M. Thomson, Proc. Roy. Soc. Tasmania, 1892, p. 12 (separate copy).

*Generic description*.—Body convex, capable of rolling into a ball, surface spiny. Metasome not abruptly contracted, terminal segment very short. Flagellum of antennæ 4-jointed. Eyes very large and prominent, on oval elevations along the sides of the head. Maxillipedes with the terminal portion large, lamellar. Legs rather short, not increasing much in length posteriorly. None of the opercular plates of the pleopoda with air-cavities. Uropoda short, not projecting much beyond the outline of the body; base broad and flattened, outer portion produced, outer ramus short, inserted at the end of the base near the inner margin; inner ramus slender.

*Remarks*.—I propose to retain the genus *Actæcia*, Dana, for the following species, and give for it the above diagnosis. In many respects it appears to resemble *Armadilloniscus*, Ulianin, with which Budde-Lund thought it to be identical, but that genus differs considerably in the form of the head and in possession of air-cavities in the first two pleopoda, and as it presumably belongs to the *Oniscidae*, it probably differs also in the terminal portion of the maxillipedes, but on this point I can get no definite information.

*Cylloma*, Budde-Lund, agrees so well with the genus in question in the eyes, and terminal uropoda and general shape, that I think it must be the same, though Budde-Lund describes it as having air-cavities in all the opercular plates of the pleopoda; this, however, perhaps arises from the fact that he had only a single badly-preserved (probably dried) specimen, and naturally thought that it belonged to the *Armadillidae* and came near to *Armadillo*.

Hayer's genus *Actoniscus* is, as he points out, nearly related to *Actæcia*, and the difference that he gives in the antennæ is more apparent than real, for *Actæcia* has only four distinct joints in the flagellum, and some of the other differences are of subsidiary importance. On the other hand, the cephalon in his species is more like that of *Armadilloniscus*, but whether it also resembles that genus in the possession of air-cavities in the first two pleopoda or not, I cannot say. In general appearance it certainly appears to resemble *Actæcia* much in the same way as *Scyphacella* resembles *Scyphax*.

The two New Zealand species of *Actæcia* may be distinguished thus:—

Eggs large, crescentic, outer branch of uropoda large, dilated distally . . . . . *A. euchroa*.  
Eyes moderate, outer branch of uropoda minute, acute at apex . . . . . *A. opitrensis*.

1. *ACTÆCIA EUCHROA*, Dana. (Plate 15. fig. 3.)

*Actæcia euchroa*, Dana, U. S. Exploring Exped., Crust. ii. p. 734, Plate 48, fig. 6 (1853).

*Actæcia euchroa*, Miers, Cat. N. Z. Crust. p. 101 (1876).

*Actæcia euchroa*, G. M. Thomson, Trans. N. Z. Inst. xi. p. 249 (1879).

*Armadilloniscus euchroa*, Budde-Lund, Isopoda Terrestria, p. 239 (1885).

*Actæcia euchroa*, Filhol, Mission de l'île Campbell, p. 443 (1885).

*Actæcia euchroa*, Thomson & Chilton, Trans. N. Z. Inst. xviii. p. 158 (1886).

*Actæcia euchroa*, G. M. Thomson, Proc. Roy. Soc. Tasmania, 1892, p. 12, Plate ii. figs. 1-8 (1892).

*Specific characters*.—Body convex, surface with short, blunt, scattered spines, especially on the margins of the metasome and on the appendages. Cephalon with the front rounded, with raised frontal margin, a little depressed in middle, a deep groove on each side interior to the prominences bearing the eyes. Inferior margin of first segment of mesosome thickened, not incised. Posterior angles of the first four segments of mesosome subquadrate, those of the last three produced backwards, subacute. Epimeral positions of third to fifth segments of metasome large and contiguous, and containing the outline of the metasome. Terminal segment very short, convex, slightly pointed between the bases of the uropoda. Eyes very large, on two crescentic prominences, occupying whole lateral border of the cephalon; ocelli very numerous, arranged in four or five longitudinal rows. Antennæ with all the joints covered with short blunt spines, flagellum about as long as preceding joint; its terminal fourth joint minute. Uropoda projecting beyond the terminal segment, and pretty accurately filling up the space between the epimera of the fifth segment; outer part of base produced into a rounded lobe, outer branch inserted on the inner portion of the distal margin, spatulate, extending a little beyond the produced portion of the base; inner rami, arising from the under surface of the base, far in front of the outer, slender, scabrous; apex with a long bristle, which is visible in dorsal view.

*Colour* light grey, with irregular black markings; during life sometimes coloured as in *Scyphax ornatus*.

*Length* about 10 mm.

*Habitat*.—Sandy beaches in New Zealand.

*Remarks*.—This species is frequently found on sandy beaches in company with *Scyphax ornatus*, and is very similar to that species in colour and habits, so that Dana thought it was perhaps the young of *Scyphax*. From what has been already said, it is clear that this is not the case, and that the two are perfectly independent; I have mature males of both species. When pursued, *Actæcia euchroa* rolls itself into a ball, and is then almost indistinguishable from a grain of speckled sand; under similar circumstances *Scyphax ornatus* crouches down closely on the sand, and is then equally difficult to perceive. I have always found these two species on the open sands and never under cover, and the large and well-developed eyes that they both possess have probably been developed in connection with their exposed mode of life.

The extremities have the usual three joints, though the articulations are not always easy to see; the last joint is tapering and bears a few setæ. The mouth-parts show a close general resemblance to those of *Scyphax*, the mandibles and first maxillæ being very similar; the appendage figured by Thomson as the inner lobe of this maxilla is really the second maxilla, which has the outer margin angularly produced near the base, and the outer lobe at the apex very small and indistinct. In the maxillipedes the ischium is distinct, but the following joints are all fused into a triangular plate with lobes on the inner margin indicating the separate joints; the masticatory lobe is small and obliquely truncate, about half as long as the terminal portion of the maxillipede. The legs have the dactyla short and stumpy-looking; the dactylar seta with distal half thickened and presenting a stippled appearance.

The first pleopoda of the male are shown in fig. 3, *plp.*<sup>1</sup> ♂; the male organ is single, broader in basal half, end with small notch; endopodite long, broad at base, apex curving a little outwards, exopodite small and oval. The endopodite of the second pleopod 2-jointed, the second forming a very long, acute process. The other pleopoda present no special features. None of them possess air-cavities so far as I can make out.

2. *ACTÆCIA OPIHENSIS*, sp. nov. (Pl. 15. fig. 4 & Pl. 16. fig. 1.)

*Specific description.*—Body very convex, rather narrow, more than twice as long as broad. Surface fairly smooth, but with numerous scattered short setæ, especially on the metasome and on the margins of the mesosome. Cephalon with the front broad, straight, with a slightly-raised transverse ridge. Posterior margins of segments of mesosome nearly straight, those of the last two a little produced backwards at the lateral angles; inferior margin of first segment thickened. Metasome convex; side portions of third to fifth segments large and recurved; terminal segment short, much broader than long, its posterior margin regularly convex. Eyes of moderate size, round. Antennæ very setose; second joint of peduncle longer than the third and nearly equal to the fourth, fifth about as long as fourth; flagellum as long as the second joint, of four joints, the first longest, second and third subequal, fourth very small. Legs setose, scarcely increasing in length posteriorly; dactylar seta large and well-marked, simple, its distal two-thirds thickened and apparently resembling a narrow circular brush. Uropoda with basal joint very large, extending beyond terminal joint, expanded and plate-like laterally; outer margin subcrenate and bearing four or five stout setæ; outer branch small, conical, scarcely projecting, tipped with a few small setæ and one or two longer ones; inner branch reaching a little beyond end of terminal segment, scabrous, and ending in two long setæ.

*Colour* yellowish, with numerous black stellate markings, some specimens nearly black.

*Size.*—Length about 6 mm.

*Habitat.*—Timaru, under seaweed at high-water mark.

*Remarks.*—I have placed this species under *Actæcia* with considerable hesitation, for it differs from the preceding species very markedly in the structure of the eyes. In external appearance it is rather like *Tylos*, but the mouth-parts are of course very different and are in fairly close general agreement with those of *Actæcia euchroa*. The terminal portion of the maxillipede is less lobed, and the masticatory lobe has a small terminal lash very like that in some species of *Trichoniscus*.

The pleopoda in the female are of usual form and apparently all similar; in each the exopodite is slightly larger than the endopodite and overlaps about half the succeeding one. In the male the first pleopoda are rather short and very strong, the endopodites in close apposition and apparently coalesced along the median line, the ends curving outwards; the second pleopod with basal portion of endopodite long, end joint not very acute.

## Family V. ONISCIDÆ.

In this family the molar tubercle of the mandible is replaced by a tuft of stiff setæ, the inner lobe of the first maxilla bears only two plumose bristles; the terminal portion of the maxillipedes is short, scarcely longer than the masticatory lobe. The uropoda are more or less exposed, and the inner ramus arises anteriorly to the outer.

The family contains numerous genera, of which four are represented in New Zealand.

## Genus 1. ONISCUS, Linné (1767).

*Oniscus*, Linnæus, Syst. Nat. ii. p. 1061 (1767).

*Oniscus*, Butc & Westwood, Brit. Sess.-eyed Crust. ii. p. 466 (1868).

*Oniscus*, Budde-Lund, Isopoda Terrestria, p. 202 (1885).

*Oniscus*, Sars, Crustacea of Norway, ii. p. 170 (1899).

*Generic description*.—"Body broad and depressed, with the lateral parts of the segments lamellarly expanded. Cephalon with well-defined lateral lobes, front imperfectly defined from the epistome. Metasome not abruptly contracted, last segment considerably produced. Eyes large, sublateral. Antennulæ with the terminal joint well developed. Antennæ slender and elongated, with the flagellum composed of three articulations. Mandibles with numerous penicils behind the cutting-part. Legs moderately slender, gradually increasing posteriorly. Opercular plates of pleopoda without any air-cavities, those of the two anterior pairs deeply bilobed. Uropoda rather produced, with the inner ramus originating far in front of the outer." (Sars.)

Although there are no actual air-cavities in the opercular plates of the first and second pleopoda in *Oniscus*, Stoller\* has recently shown that in the outer portion of these plates there is a structure which performs the same function of allowing the animal to breathe ordinary dry air.

## 1. ONISCUS PUNCTATUS, G. M. Thomson (1879). (Pl. 16. fig. 2.)

*Oniscus punctatus*, G. M. Thomson, Trans. N. Z. Inst. xi. p. 232, pl. x a. fig. 3 (1879).

*Oniscus punctatus*, Budde-Lund, Isopoda Terrestria, p. 206 (1885).

*Oniscus punctatus*, Filhol, Mission de Pile Campbell, p. 440 (1885).

*Oniscus punctatus*, Thomson & Chilton, Trans. N. Z. Inst. xviii. p. 158 (1886).

*Specific description*.—Body oblong-oval, rather more than twice as long as broad, rather convex, whole surface covered with short setæ which in dried specimens give the appearance of small scale-like markings. Cephalon with the front depressed, produced slightly into an obtuse lobe; lateral lobes small, ending subacutely. Mesosome with the posterior margins of the first three segments straight and their posterior angles rectangular; lateral angles of last four segments produced more and more backwards, acute. Epimera of third to fifth segments of metasome well developed, narrow, ending acutely; terminal segment not much produced, triangular, much broader than long, the rounded apex reaching as far as the end of the base of the uropoda and bearing a few minute setæ which scarcely project beyond its margin.

\* Zoologica, Heft xxv. (1899).

Eyes of moderate size, with fifteen to twenty ocelli. Antennæ as long as the head and first three segments of mesosome minutely setose throughout; second and third joint subequal, fourth longer, fifth twice as long as the fourth and longer than the flagellum; joints of flagellum increasing in length distally, and the third followed by a styliform process or bristle, fully as long as the first joint and dividing at the end into a compact pencil of setæ. Legs fairly long and very spinous, increasing considerably in length posteriorly. First two pairs of pleopoda with the opercular plates partially bilobed. Uropoda with the outer joint much longer and stouter than the inner, which arises only a little anterior to it and reaches to the middle of the outer, both setose and bearing one or two longer setæ at the end.

*Colour* brown, with wavy stripes of white on each side the median line and often with two lateral rows of whitish patches, the number and size of the white markings varying greatly.

*Length* about 10 mm.

*Habitat*.—Very common throughout the whole of New Zealand.

*Remarks*.—I have had some little hesitation in referring it to the genus *Oniscus* as now restricted, for it differs distinctly from the definitions of that genus as given both by Budde-Lund and by Sars in that the mandibles do not bear so many "penicils" behind the cutting-part; I find only *one* on each mandible, though another one or sometimes two are situated on the setose membranaceous lappet just internal to the cutting-edge. According to Budde-Lund *Oniscus* should have four or five penicils. Moreover, the anterior segments of the mesosome have the posterior margin straight instead of deeply sinuate, and the last segment is broader and less produced than is usual in *Oniscus*. Budde-Lund (p. 206) suggests that the species under consideration may belong to *Philoscia*, and it certainly agrees with that genus in the mandibles and in the posterior margins of the segments of the mesosome, but it differs from that genus in possessing well-marked though small lateral lobes on the cephalon, and in having the epimera of the mesosome of fair size, and those of the third to fifth segments of metasome well marked. On the whole I prefer to leave the species under *Oniscus*, for though allied genera are plentiful enough I cannot at present find one that will suit it better.

The species is widely distributed throughout New Zealand, and presents considerable variation in colour, breadth, and compactness of the body prominence of the front and lateral lobes, &c. I have some specimens collected by Mr. W. W. Smith on limestone rocks at Albury, Canterbury, which in colour resemble the variety *marmoratus* of *Porcellio scaber*, the general surface being very light yellow, marked with somewhat sparsely-scattered black dots and markings; the small spines on the surface are more marked than in typical specimens, the front is less produced, and the lateral lobes of the cephalon are very small and inconspicuous, while the joints of the flagellum of the antennæ are more equal in length. In other respects they resemble *Oniscus punctatus* so closely that I prefer, for the present at any rate, to consider them merely as a variety of that species, for which I propose the name *marmoratus*.

The specimens from Mount Wellington, Tasmania, referred to this species by



Mr. Thomson \*, differ in having the side-plates of the third to fifth segments of the metasome much smaller, and thus approach still more closely to *Philoscia*, under which they should perhaps be placed.

2. *ONISCUS KENEPURENSIS*, sp. nov. (Pl. 16. fig. 3.)

*Specific description*.—Body regularly oblong-oval, broad, the length rather less than twice the greatest breadth; dorsal face but slightly convex, finely granular, not setose, each segment bearing on each side of the median line a slightly raised and wrinkled patch, most marked on anterior segments. Cephalon small, deeply sunk into first segment of pereion, frontal edge regularly convex; lateral lobes very small, subacute at apex. Side-plates of mesosome greatly prominent, lamellar, contiguous, projecting almost laterally, those of the first segment extending forwards into subacute lobes, which reach to the level of the anterior margin of the eyes; posterior angle broadly rounded; posterior margins of the second and third segments slightly sinuous; posterior angles rectangular, slightly rounded. Posterior angles of the fourth to seventh segments progressively produced more and more backward and ending acutely; those of the seventh reach as far posteriorly as the end of the epimeral portion of the third segment of metasome. First two segments of metasome of fair length, but wholly embraced by the preceding segment; epimeral plates of the next three segments produced and recurved, ending acutely, the last reaching slightly beyond the end of the terminal segment. Terminal segment triangular, broader than long, sides slightly concave, end rounded and reaching as far as the end of the base of the uropods, posterior portion slightly depressed and concave.

Eyes of moderate size, about fifteen ocelli. Antennæ very similar to those of *Oniscus punctatus*, scabrous, the minute setæ being less prominent than in that species. Legs long, spinose, the posterior pairs somewhat elongated. Opercular plates of pleopoda not bilobed. Uropoda with basal joint large; outer ramus broad at base, tapering regularly and equally on both sides to an acute point, scarcely setose, inner ramus reaching to the middle of the outer, minutely setose.

*Colour*.—Slate-coloured, with white markings on the wrinkled patches on the mesosome and usually with a lateral row of white patches at junction of epimera with the central portion.

*Length* about 11 mm., breadth 6·5 mm.

*Habitat*.—Kenepuru (*J. McMahon*).

*Remarks*.—In fully-grown specimens this species can be readily distinguished from *Oniscus punctatus* by the flattened body, the greatly-developed epimera, and the wrinklins on the dorsal surface; in younger forms all of these points are less marked, but the species can then be usually recognized by the large and acutely-pointed outer rami of the uropods.

\* Proc. Roy. Soc. Tasmania, 1892, p. 10 (separate copy).

3. *ONISCUS COOKII*, Filhol.

*Oniscus Cookii*, Filhol, Mission de l'île Campbell, 1885, p. 442, pl. 54, fig. 6.

The following is the description given of this species by Filhol :—

“ J'ai recueilli cette espèce sous les pierres sur la portion ouest de l'île du milieu de la Nouvelle-Zélande. Elle ne mesure que 0<sup>m</sup>.008 de longueur et 0<sup>m</sup>.004 de largeur. Le corps est ovalaire et remarquablement bombé; la tête est large, les antennes externes sont très fines et leur cinquième article plus développé à la longueur du flagellum. Il n'existe pas de poils ni sur les articles basilaires des antennes externes, ni sur le flagellum. La base des articles composant les antennes est brune, alors que le sommet est blanc. Les anneaux du thorax sont assez développés d'avant en arrière. Ils sont couverts, en grande partie, de très fines granulations d'une teinte noire. Les granulations font défaut en différents points des anneaux et, là où elles manquent, on observe des surfaces un peu creusées, d'une teinte noisette. Ces surfaces dénuées de granulations, et apparaissant en creux à cause des saillies que font les granulations qui les limitent, sont de formes très variables. Tantôt elles sont arrondies, tantôt elles se divisent et figurent de grossières arborisations. Sur les anneaux de l'abdomen on retrouve ces plaques, mais elles sont alors granuleuses, comme le reste des anneaux qui les présentent. Les stylets externes sont les plus développés et leur bord externe est garni, ainsi que celui des stylets internes, de soies très-fines, courtes et très serrées.”

I cannot recognize this species unless, indeed, it be *Oniscus kenepurensis*.

Genus 2. *PHILOSCIA*, Latreille (1804).

*Philoscia*, Latreille, Hist. des Crust. &c. t. 7, p. 43 (1804).

*Philoscia*, Bute & Westwood, Brit. Seas.-eyed Crust. ii. p. 418 (1868).

*Philoscia*, Budde-Lund, Isopoda Terrestria, p. 207 (1885).

*Philoscia*, Sars, Crustacea of Norway, ii. p. 172 (1899).

*Generic Characters*.—Body oval, slightly convex, with rather thin integuments. Cephalon rounded in front, without any projecting lateral lobes. Side-plates of mesosome but slightly prominent. Metasome abruptly contracted, with the epimeral plates small and appressed; last segment not much produced. Eyes well developed, lateral. Antennæ very slender, with the flagellum composed of three articulations. Mandibles with only a single penicil behind the cutting-part. Legs very slender and greatly increasing in length posteriorly. Opercular plates of pleopoda without any air-cavities and scarcely bilobed. Uropoda not much produced, with the inner ramus not attached so far in front as usual. [Sars, *l. c.* p. 173.]

1. *PHILOSCIA PUBESCENS*, Dana. (Pl. 16, fig. 4.)

*Oniscus pubescens*, Dana, U. S. Explor. Exped., Crust. ii. p. 730, pl. 48, fig. 2 (1853).

*Oniscus pubescens*, Miers, Cat. N. Z. Crust. p. 99 (1876).

*Philoscia mina*, Budde-Lund, Isopoda Terrestria, p. 219 (1885).

*Philoscia pubescens*, Budde-Lund, Isopoda Terrestria, p. 223 (1885).

*Oniscus pubescens*, Filhol, Mission de l'île Campbell, p. 440 (1885).

*Oniscus pubescens*, Thomson & Chilton, Trans. New Zealand Inst. xviii. p. 158 (1886).

*Philoscia mina*, Dollfus, Bull. Soc. Zool. de France, xviii. p. 168 (1893).

*Specific description.*—Body narrow oblong-oval, surface smooth and shining in large specimens, in small specimens bearing numerous short setæ. First and second segments of mesosome with posterior margins straight, lateral angles rounded, posterior margin of third slightly sinuate, posterior angles of last three segments only slightly produced backward, subacute. Metasome abruptly narrower than mesosome; epimera of third to fifth segments small, closely appressed. Terminal segment triangular, flat, sides straight or a little incurved, apex subacute.

Antennæ very long and slender, from one-half to two-thirds the length of the body, very hirsute, especially towards the end and in small specimens; third and fourth joints together equal in length to the fifth, which is as long as the flagellum, the three joints of which are subequal; terminal stylet slender, about two-thirds the length of the last joint. Legs long, greatly increasing in length posteriorly, very spinous. Opercular plates of the second and succeeding pleopoda with three or four setæ projecting at right angles to the surface. Basal joint of uropoda reaching well beyond the last segment; inner surface scabrous and with a few setæ; outer side with a well-marked groove, becoming shallower towards the base; inner branch rather more than half as long as the outer, arising only a little in front of it, with numerous short setæ and two longer ones at the apex; outer ramus much stouter and conical, scabrous, and with some small setæ but fewer than on the inner ramus.

*Colour* light brown, often whitish, with various markings of darker brown, arranged roughly in a median and two lateral longitudinal bands, frequently with a row of whitish patches at the bases of the epimera. Legs yellowish white with brown markings, especially on the basal joints.

*Length* about 10 mm., breadth 4 mm.

*Habitat.*—Under rotten wood in forests, Whykare River (*Dana*); Howick, Auckland (*G. M. Thomson*); Takapuna (*L. Hames*); Kenepuru, Marlborough (*J. McMahon*).

*Remarks.*—I have little doubt that the specimens which I have described above are to be considered as belonging to *Oniscus pubescens*, Dana. From his description and figures it is evident, as Budde-Lund has already inferred, that he was dealing with a species of *Philoscia*. His figure shows an Isopod less narrow than most of my specimens, but it was taken from a specimen only 3 mm. long, and I have specimens of about the same size that correspond very closely to his figure, and from the series at my command I am able to record the fact that in young specimens the metasome may be only as long as it is broad at the base, while in larger specimens it may be fully twice as long as broad, and that the mesosome shows corresponding variations; in large forms, too, the antennæ become longer and more slender. Dana's specimens were obtained from the north of Auckland, and most of my specimens are also from places not very far removed where the species appears to be fairly common, and I know of no other species from that neighbourhood to which Dana's description could apply.

I have little doubt that the species described by Budde-Lund from the Cape of Good Hope under the name *Philoscia mina*, and afterwards recorded by Dollfus from three localities in the Seychelles, is the same as the New Zealand species. Budde-Lund's description applies well to my specimens, and the groove on the outer surface of the base of the

uropoda appears very characteristic. Dollfus's figure is very like that of my larger specimens, though the closely-appressed epimera of the metasome are not shown, and in accordance with what I have said the metasome is shown narrower than it is in young specimens. Dollfus calls attention to the fact that while Budde-Lund described the surface as glabrous, his specimens "présentent au contraire des poils épars, qui paraissent, il est vrai, assez caducs." I am able to explain the inconsistency, for my specimens show that while the smaller specimens (even sexually mature) usually possess numerous scattered setæ, the largest specimens have the surface nearly or quite glabrous.

I give figures of the first and second pleopoda of the male, which are of much the usual type and do not call for special description. Attached to the male organ in connection with the first pleopod is the vas deferens and apparently a large portion of the testes, which came away with it when I dissected off the pleopod.

## 2. *PHILOSCIA NOVÆ-ZEALANDIÆ*, Filhol.

*Philoscia novæ-zealandiæ*, Filhol, Mission de l'île Campbell, 1885, p. 144, pl. 54. fig. 2.

Filhol gives the following description of this species :—

"Cette espèce, que je crois nouvelle, a le corps allongé, ovalaire, assez bombé dans la portion médiane. Les antennes externes sont couvertes sur leurs bords antérieur et postérieur et sur leur face externe de poils courts, très fins, très serrés et ayant dans leur forme, leur disposition quelque chose qui rappelle de petites épines. Les segments du thorax sont granuleux sur presque toute leur étendue et les granulations sont d'un brun noirâtre. Là où elles font défaut la carapace est d'une teinte jaune clair. Les parties granuleuses sont disposées de telle manière qu'elles constituent tout le long du corps de l'animal trois sortes de bandes noirâtres ; l'une médiane, les deux autres latérales. Les stylets caudaux externes sont un peu plus longs que les stylets caudaux internes, mais ils sont tous couverts de poils très fins sur toute leur surface. Il existe une ligne de ponctuations noires le long du bord externe des stylets externes.

	m.	m.
Longueur . . . . .	0.022	à 0.026.
Largeur . . . . .	0.008	à 0.009.

J'ai trouvé cette espèce aux environs de Wellington dans l'île du Nord, aux environs de Dunedin dans la province d'Otago et enfin dans l'île Stewart."

I cannot identify this with any species known to me ; the figure shows the side-plates of the metasome much larger than is usual in *Philoscia*, but does not help in deciding what the species Filhol had before him.

## Genus 3. *PORCELLIO*, Latr., 1804.

*Porcellio*, Spence Bate & Westwood, British Sessile-eyed Crustacea, ii. p. 473 (1868).

*Porcellio*, Budde-Lund, Isopoda Terrestria, p. 82 (1885).

*Porcellio*, Stebbing, History of the Crustacea, p. 426 (1893).

*Porcellio*, G. O. Sars, Crustacea of Norway, ii. p. 176 (1899).

The following are the generic characters as given by Sars:—

“Body oval, more or less depressed, with the lateral parts lamellarly expanded. Cephalon partly flanked by the side-plates of the first segment of mesosome, lateral lobes well developed, frontal lobe more or less projecting, and distinctly defined from the epistome. Metasome not abruptly contracted, epimeral plates of the third to fifth segments prominent and recurved; last segment conically produced. Eyes, as a rule, well developed, subdorsal. Antennæ moderately slender, with the flagellum composed of two articulations only. Oral parts normal. Legs gradually increasing in length posteriorly, last pair in male sometimes slightly differing from that in female. Opercular plates of the two anterior pairs of pleopoda, and sometimes of the three succeeding pairs, provided with distinct air-cavities. Copulative organs of male of a similar structure to that in *Oniscus*. Uropoda distinctly projecting, outer ramus lanceolate, inner much smaller, linear, and originating far in front of the former.”

#### PORCELLIO SCABER, Latr.

*Porcellio scaber*, Latreille, Hist. Nat. des Crustacés et des Insectes, vol. vii. p. 45.

*Porcellio scaber*, Spence Bate & Westwood, British Sessile-eyed Crustacea, ii. p. 475 (1868).

*Porcellio graniger*, White, List. Crust. Brit. Mus. p. 99 (1847), *sine descr.*

*Porcellio graniger*, Miers, Ann. Mag. Nat. Hist. (ser. 4) xvii. p. 226 (1876), and Cat. New Zealand Crustacea, p. 99 (1876).

*Porcellio graniger*, Budde-Lund, Isopoda Terrestria, p. 129 (1885).

*Porcellio graniger*, Budde-Lund, l. c. p. 149 (1885).

*Porcellio graniger*, Thomson & Chilton, Trans. N. Z. Inst. xviii. p. 158 (1886).

*Porcellio graniger*, Haswell, Cat. Australian Crust. p. 280.

*Porcellio graniger*, G. M. Thomson, Proc. Royal Soc. Tasmania, 1892. p. 4.

*Porcellio scaber*, Stebbing, History of the Crustacea, p. 427 (1893).

*Porcellio scaber*, G. O. Sars, Crustacea of Norway, ii. p. 176 (1899).

*Specific Characters*.—“Body oblong-oval, about twice as long as it is broad, dorsal face slightly convex and very rough, owing to the presence of numerous rounded tubercles. Cephalon with the lateral lobes rather large and rounded, frontal lobe less prominent, obtusely triangular. Side-plates of mesosome of moderate size, with the posterior corners acutely produced. Metasome occupying about one-quarter of the length of the body; epimeral plates of the third to fifth segments strongly recurved; last segment rather produced, terminating in an acute point slightly grooved dorsally. Antennæ less slender, scarcely attaining half the length of the body; flagellum about as long as the last peduncular joint, and having its two articulations of nearly equal size. Last pair of legs differing but little in the two sexes. Opercular plates of only the two anterior pairs of pleopoda with air-cavities. Uropoda with the outer ramus broadly lanceolate, and comparatively larger in male than in female. Colour of dorsal face generally of a uniformly greyish black; sometimes, however, lighter, and variegated with irregular dark patches, more rarely black, with the side plates light yellowish. Length of adult female 14 mm.” (Sars.)

*Habitat*.—Found in great abundance throughout the whole of New Zealand, especially around buildings, in greenhouses, &c.; rarely in the native bush.

*Remarks*.—This species is practically cosmopolitan, being found all over Europe, North America, at the Cape of Good Hope, and Kamtschatka. In Australia it has been recorded from Melbourne and Tasmania, and I have specimens from Sydney also. In New Zealand it has hitherto been known under the name *Porcellio graniger*, Miers, though Mr. G. M. Thomson suggested some years ago that it was probably a cosmopolitan species, and pointed out how easily it might be spread by artificial means\*. Budde-Lund, in his "Isopoda Terrestria," had previously suggested that the New Zealand species was perhaps the same as *P. leviss*, Latr., but a comparison of specimens has shown that it differs considerably from that cosmopolitan species, but is undoubtedly the same as *P. scaber*, Latr.

The variety *marmorata*, in which the general dorsal surface is lightly coloured and variegated with irregular dark patches, is pretty abundant in New Zealand, and the variety *marginata* "black, with side-plates light yellowish," is also sometimes seen. Some years ago Mr. W. W. Smith sent me a large series of specimens from Ashburton, some of the usual form (variety *immaculata*), others of the variety *marmorata*, and a large number with the whole dorsal surface (in spirit) of a reddish-brown varying from a light yellowish-brown to dark orange-brown, some of them having the side-plates lighter in colour than the centre portion; there is a similar specimen in Mr. Thomson's collection, and I have occasionally seen similar specimens from other localities; in this form the tubercles on the dorsal surface are hardly so well marked as in some of the darker forms belonging to the variety *immaculata*, but there seems to be considerable variation in the degree of tuberculation in all the varieties.

Many years ago Brandt described albino and partially albino forms of this species, and gave figures showing all the stages between complete albinos and the ordinary dark-coloured forms†.

The great variability in colour of this species has been noted by Filhol in specimens collected from New Zealand.

#### Genus 4. METOPONORTHUS, Budde-Lund, 1879.

*Metoponorthus*, Budde-Lund, *Isopoda Terrestria*, p. 161 (1885).

*Metoponorthus*, Sars, *Crustacea of Norway*, ii. p. 183 (1899).

*Generic Characters*.—"Body oblong, subdepressed, with very thin integuments. Cephalon with the lateral lobes very small, frontal lobe obsolete. Side-plates of mesosome but very slightly prominent. Metasome abruptly contracted, with the epimeral plates of third to fifth segments sub-appressed; last segment comparatively short, triangular. Eyes well developed, lateral. Antennulæ very small, with the last joint quite short. Antennæ slender and elongated, flagellum biarticulate. Oral parts nearly exactly as in *Porcellio*. Legs slender, and greatly increasing in length posteriorly.

\* "Proc. Royal Society Tasmania," 1892, p. 4 (separate copy).

† *Hort. Soc. entom. Ross. T. viii.* (1871), pp. 167-176, 1872.



Opercular plates of the two anterior pairs of pleopoda with air-cavities, more rarely also those of third or of all pairs. Copulative organs of male nearly as in *Porcellio*. Uropoda rather produced, and of a similar structure to that in *Porcellio*."

1. ? *METOPONORTHUS PRUINOSUS*, Brandt.

*Porcellio pruinus*, Brandt, Consp. monogr. Crust. Isop. terrestr. p. 19, fig. 21.

*Porcellio zealandicus*, White, List. Crust. Brit. Mus. p. 99, 1847 (*sine descrip.*) ; Miers, Cat. N. Z. Crust. p. 100 (1876).

*Metoponorthus pruinus*, Budde-Lund, Isopoda Terrestria, p. 169 (1885).

*Porcellio neo-zealandicus*, Thomas & Chilton, Trans. N. Z. Inst. xviii. p. 158 (1886).

*Metoponorthus pruinus*, Sars, Crustacea of Norway, ii. p. 184 (1899).

Budde-Lund gives *Porcellio zealandicus*, White, as a doubtful synonym of *Metoponorthus pruinus*, Brandt. I have seen the type specimen in the British Museum; it is dried and not very well preserved, but is undoubtedly a *Metoponorthus*, and apparently very closely resembles *M. pruinus*. It would certainly not be extraordinary if this cosmopolitan species were found in New Zealand, but I have never met with it, though White's specimen, if really from New Zealand, must have been collected there before 1847, and we might naturally have expected that the species would have become abundant since then.

To make the account of this species complete, I quote here the description given of it by Miers:—

"Elongate oblong, finely granulous, the granules seriate on the posterior margin of each segment. Head small, transversely oblong, with the latero-anterior angles not prominent. Segments of the thorax (the last excepted) with the posterior and infero-lateral margins straight, the infero-posterior angles obtuse; last segment of thorax broad, with the posterior margin concave, the infero-lateral margin straight, the infero-posterior angle acute. Segments of the abdomen considerably narrower than those of the thorax, short; terminal segment equilaterally triangular, slightly concave above, sides straight. Caudal appendages with the base shorter than the terminal segment, the longer (exserted) ramus narrow, acute, projecting beyond the terminal segment to a distance equal to its own length. External antennæ very long and hairy—length nearly one-third inch. New Zealand (Coll. Brit. Mus.)."

Family VI. ARMADILLIIDÆ.

In this family the body is generally convex, and the animals capable of rolling up into a ball; the metasome is not abruptly narrower than the mesosome. There are air-cavities in two or more of the outer branches of the pleopoda, and the uropoda are usually short and not produced beyond the terminal segment. In other respects the family resembles the *Oniscidæ*, with which it is so connected by some intermediate genera that, as Sars has pointed out, it is rather difficult to get points of difference that will apply in all cases.

The family contains many genera, several of which have been established during

recent years by M. Adrien Dollfus, but all the New Zealand species appear to be referable to *Armadillidium* and *Armadillo*.

Genus 1. ARMADILLIDIUM, Brandt, 1830.

*Armadillidium*, Budde-Lund, Isopoda Terrestria, p. 49 (1885).

*Armadillidium*, Dollfus, Feuille des Jeunes Naturalistes, iii<sup>e</sup> Série, 1<sup>er</sup> Mai 1892, No. 259 (1892).

*Armadillidium*, Sars, Crustacea of Norway, ii. p. 188 (1899).

*Generic Characters*.—"Body oblong or elliptical in form, very convex, and capable of being rolled up into a perfect ball. Cephalon with the front distinctly marginate, lateral lobes rounded and sharply defined at the base. Epistome vertical, forming above a triangular shield, advancing more or less beyond the frontal edge. Side-plates of first segment of mesosome large, securiform, not incised behind. Metasome semicircular, with the edges continuous throughout; last segment lamellar, quadrangular or triangular in form, not extending beyond the limits of the epimeral plates of the penultimate segment. Eyes distinct, lateral. Antennule with the terminal joint but little produced. Antennæ, as a rule, not attaining half the length of the body, penultimate peduncular joint scarcely longer than the second; flagellum biarticulate. Opercular plates of only the first two pairs of pleopoda with air-cavities. Uropoda very short, with the basal part broad, lamellar, outer ramus spatulate, inner narrow, cylindric." (Sars.)

1. ARMADILLIDIUM VULGARE, Latr.

*Armadillo vulgaris*, Latreille, Hist. Crust. vol. vii. p. 48.

*Armadillo vulgaris*, Bate & Westwood, Brit. Sess.-eyed Crust. ii. p. 492 (1868).

*Armadillidium vulgare*, Budde-Lund, Isopoda Terrestria, p. 66 (1885).

*Armadillidium vulgare*, Dollfus, Feuille des Jeunes Naturalistes, iii<sup>e</sup> Série, No. 259 (1<sup>er</sup> Mai 1892).

*Armadillidium vulgare*, Sars, Crustacea of Norway, ii. p. 189 (1899).

*Specific Characters*.—"Body oblong-oval, more than twice as long as it is broad, side-contours sub-parallel, dorsal face strongly vaulted and perfectly smooth. Cephalon, seen dorsally, broadly quadrangular, transversely truncated in front, lateral lobes comparatively small, rounded. Side-plates of first segment of mesosome with the posterior corner acute. Metasome broad, semicircular, scarcely occupying more than one-fifth of the length of the body; last segment much shorter than it is broad at the base, and slightly tapering distally, tip transversely truncated. Antennæ very short, scarcely exceeding in length one-quarter of the body; flagellum about the length of the last peduncular joint, and having its first articulation somewhat shorter than the second. Last pair of legs with the ischial joint rather large, equalling in length the succeeding part of the leg. Copulative appendages of the first pair of pleopoda in male with the tips slightly divergent; opercular plate of the second pair rather produced, but scarcely curving outwards at the tip. Uropoda with the outer ramus much shorter than the basal part, and very broad, its distal edge being continuous with the last segment. Colour of distal face somewhat variable, sometimes uniformly dark grey or nearly black, sometimes variegated with lighter patches, generally arranged on the mesosome in three longitudinal rows, one median and two lateral; between them, moreover, on each

segment is a group of more or less distinct flexuous stripes. Length attaining 14 mm." (Sars.)

*Habitat*.—Nelson (J. C. Gully), and Mount Egmont (S. H. Drew).

*Remarks*.—I have a few specimens from Nelson and one from Mount Egmont that undoubtedly belong to this species, which is very widely distributed throughout all Europe, and the adjacent parts of Asia and Africa. According to Budde-Lund it has also been widely dispersed, probably by artificial means, and has been found at New York, Monte Video, Melbourne, &c. It has not been previously recorded from New Zealand, and it is a little strange that it should have been taken at Nelson and Mount Egmont, when it has not yet been found at any of the chief ports or in other parts of the Islands.

My specimens agree very closely with the figures and descriptions given by Sars and Dollfus, and I have been able to compare them with specimens from England, and can find no points of difference between them. In the male the first pair of legs has the carpus a little more swollen than is shewn in Sars' figure, and has the propodos bent back upon it so as to form an imperfectly subchelate hand. I find, however, that the degree to which this structure is developed varies in different individuals, and it is perhaps fully developed only in the adult male, or perhaps only during the breeding season. The long ischium of the seventh pair of legs is also a characteristic of the fully-grown male; in the females it is only of normal length; in the male, too, the meros and carpus of the first six pairs of legs, and especially of the fourth, fifth and sixth, are much more setose than in the female.

With regard to the colour, Budde-Lund distinguishes two varieties: first, *immaculata*, "e plumbeo griseus," and second, *variegata*, "annulorum marginibus albis serieque dorsali triplici vel quadruplici macularum flavarum." Dollfus, who has given a detailed account of this species in the work quoted, says: "Les ♂ sont généralement d'un gris uniforme, ou avec quelques taches safranées; les ♀ d'un brun plus ou moins clair, avec des taches et marbrures pâles." The few specimens that I have from New Zealand are all males, and are of a uniform dark slaty-grey colour.

## Genus 2. ARMADILLO.

*Armadillo*. Budde-Lund, *Isopoda Terrestria*, p. 35 (1885).

*Generic Characters*.—Resembling *Armadillidium* in most respects, but with the shield on the epistome much less marked, and the grooves for the antennæ consequently very shallow; the side-plates of the first segment of the mesosome usually, and those of the second segment sometimes, incised or grooved; the last segment of metasome subtetragonal, broader at the base than apex, sides concave; the outer branches of all the pleopoda with air-cavities: uropoda with the base large, flattened and produced so as to fill up the space between the side-plates of the fifth segment and the terminal segment; outer branch small, inserted on inner margin of the enlarged base; inner branch arising more anteriorly, quite concealed in dorsal view by the terminal segment.

This genus contains many species, a large proportion of which are found, as Budde-

Lund says, on the islands and shores of the Pacific. In New Zealand there are at least six species which may be distinguished as follows :—

A. Surface of body nearly smooth.

I. Inferior margin of first segment of mesosome simple.

a. Outer branch of uropoda very small, rudimentary . . . . . *A. speciosus*.

b. Outer branch of uropoda of moderate size . . . . . *A. ambitiosus*.

II. Inferior margin of first segment of mesosome grooved along its whole length . . . . . *A. Danae*.

III. Margin of first segment of mesosome notched behind . . . . . *A. rugulosus*.

B. Surface of body with crests or tubercles.

I. Surface with numerous thin crests or flange-like processes . . . . . *A. Hamiltoni*.

II. Surface with setose tubercles.

a. Tubercles large, about four on each segment of mesosome . . . . . *A. Macmahoni*.

b. Tubercles small, acute, numerous . . . . . *A. spinosus*.

1. ARMADILLO AMBITIOSUS, Budde-Lund. (Plate 16. fig. 5.)

*Armadillo ambitiosus*, Budde-Lund, Prospectus Crust. Isop. terr. p. 7 (1879); Isopoda Terrestria, p. 34 (1885).

*Specific description*.—Body oval, very convex, nearly smooth, minutely punctate. Dorsal surface of cephalon marked off from the pre-epistome by a well-marked ridge, which at the sides projects a little above the surface of the cephalon, centre usually a little depressed; dorsal surface smooth or a little uneven, pro-epistome smooth, flat. Inferior margin of first segment of mesosome thin, with a small tooth posteriorly on the inner surface; second segment with the inferior margin entire, thicker in front, the thickened part ending abruptly in a small tubercle on the inner surface at some little distance from the margin. Posterior margins of the anterior four segments sinuate, posterior angle of first produced backwards subacute, that of second a little produced. Terminal segment of metasome a little longer than its breadth at base, narrowing abruptly, the posterior portion with sides parallel or slightly divergent; posterior margin truncate, slightly rounded or squarely truncate, often with a very small emargination in the centre.

Antennæ minutely setose, flagellum as long as fourth joint of peduncle, and shorter than the fifth, its second joint three times as long as the first, apex with styliiform appendage about as long as first joint. Eyes somewhat large, with about 20 ocelli. Basal joint of uropoda with the portion exposed dorsally narrow, about twice as long as broad, end sharply rounded; exterior ramus slender, arising from well-marked notch on inner margin of base, not reaching quite to the end of base; inner branch a little shorter than the terminal segment. Colour usually brownish, varying considerably in depth of tint, usually with wavy markings of a lighter colour on each side of median line.

*Length* up to 15 mm., breadth about 7 mm., height 3·5 mm.

*Habitat*.—Widely distributed in North Island; also found at Greymouth and Kenepuru.

*Remarks*.—This is a widely-spread species, and appears to show considerable variation. It is quite possible that I am including under it forms that others might look upon as separate species, but my difficulty has been that if I divide it up at all, I

would require to establish at least four or five new species for its members, and I shrink from such an undertaking.

In specimens that I look upon as typical forms the whole surface of the head and body is smooth, the ridge along the front of the cephalon is not very prominent, especially in the centre, the end of the last segment is nearly straight (corners rounded) and with indication of a slight emargination in the centre, and the "tooth" on the inner side of the lateral margin of the first segment, and the small tubercle on that of the second, are fairly distinct. I have some specimens from Greymouth, where the ridge along anterior border of head is much more pronounced, the "tooth" and "tubercle" less evident, end of last segment slightly rounded with no indication of emargination; the surface of the head, moreover, presents some slight irregularities, and there are a few indistinct wavy elevations on the sides of the median line of the body; the central part of the last segment is a little raised, though hardly sufficient to be called ridged, and the basal portion of the last segment, and the epimeral portions of the third to fifth segments of the metasome, are rather broader than in the type.

Two specimens from Wanganui in Mr. Thomson's collection agree with these Greymouth specimens in the ridge on the anterior margin of cephalon, and in the "tooth and tubercle," but the epimeral portions of metasome and the basal portion of the uropoda are fully as narrow as in the typical specimens; the end of last segment is quite squarely truncate, and the whole body is nearly smooth. In these two specimens the inner branch of the uropoda is shorter than in any other I have seen.

Specimens from other localities show other combinations of these various characters, and on the whole I think it wisest to consider them all as belonging to one species.

## 2. ARMADILLO DANÆ, Heller.

*Spherillo danæ*, Heller, Reise der Novara, p. 134, pl. xii. fig. 4 (1865).

*Armadillo inconspicuus*, Miers, Ann. & Mag. Nat. Hist. ser. 4, xvii. p. 225 (1876); Cat. N. Z. Crust. p. 95, pl. ii. fig. 4 (1876).

*Spherillo danæ* et *Armadillo inconspicuus*, Thomson & Chilton, Trans. N. Z. Inst. xviii. p. 159 (1886).

*Armadillo danæ*, Budde-Lund, Isopoda Terrestria, p. 39 (1885).

*Armadillo inconspicuus*, Budde-Lund, l. c. p. 39 (1885).

*Armadillo inconspicuus*, Filhol, Mission de l'île Campbell, p. 439 (1885).

*Spherillo danæ*, Filhol, l. c. p. 440 (1885).

*Specific description*.—In the cephalon surface and general appearance closely resembling *A. ambitiosus*. Posterior border of first segment of metasome only very slightly produced backwards, that of others straight. Lateral margin of first segment with a narrow groove extending along its whole length, becoming shallower anteriorly, second segment also with lateral margin deeply grooved. Segments of metasome short, epimeral portions less elongated than in *A. ambitiosus*, terminal segment a little broader at base than at the extremity, end truncate, slightly rounded.

Basal portion of uropoda with exposed portion small, end rounded, outer ramus minute, inner ramus reaching very nearly to the end of last segment.

*Colour* brownish, with lighter wavy markings on each side the median line.

*Length* about 10 mm.

*Habitat*.—Takapuna, Auckland (L. Hames); Auckland (Heller), Bay of Islands (Dana). Filhol says that he has found this species in great abundance in the North Island, and that it becomes less and less abundant towards the south, though he gathered a few examples of it on Stewart Island. The statement as to the greater abundance in the north is also true of *Armadillo inconspicuus*, which this species closely resembles, and there is nothing to show definitely that Filhol distinguished the one from the other.

I have a single specimen of this species before me from Takapuna, Auckland, and have no difficulty whatever in identifying it with *A. inconspicuus*, Miers. It also agrees very well with Heller's description, if we remember that the part he speaks of as the outer branch of the uropoda is the outer distal portion of the base, and that his "inner branch" is really the outer, though, as usual in this genus, arising from the inner margin of the produced portion of the base.

In colour and general appearance this species is very like *A. ambiguus*, Budde-Lund, but it may be readily distinguished from that species by the groove on the lower margin of the first segment of the mesosome, and by the minute outer branch of the uropoda.

### 3. ARMADILLO SPECIOSUS, Dana. (Pl. 16. fig. 6.)

*Armadillo speciosus*, Dana, U. S. Explor. Exped., Crust. ii. p. 718, pl. 47. fig. 2 (1853).

*Armadillo speciosus*, Miers, Cat. N. Z. Crust. p. 95 (1876).

*Armadillo speciosus*, Budde-Lund, Isopoda Terrestria, p. 39 (1885).

*Armadillo speciosus*, Filhol, Mission de l'île Campbell, p. 439 (1885).

*Specific description*.—Body very convex. Cephalon with frontal margin raised, a little interrupted in the centre. Segments of mesosome each with transverse row of indistinct tubercles or granules; inferior margin of first segment simple, curving a little outwards. Segments of metasome in close contact, the last nearly as broad at apex as at the base; sides concave, posterior margin straight. Uropoda with the outer joint minute, rudimentary, inner branch slender, extending to the end of last segment.

*Colour* light reddish brown, with darker markings.

*Length* about 6 mm.

*Habitat*.—Bay of Islands (Dana); Chatham Islands (Hutton).

*Remarks*.—I have three or four specimens (mostly imperfect) from Chatham Islands that I have little hesitation in assigning to Dana's species. He describes his genus *Armadillo* as having the external ramus of the uropods obsolete, and figures his species *A. speciosus* in accordance with this view. It is true that in the specimens before me the outer branch is present, but it is so minute that it would be impossible to show it in a figure the same size as that which Dana gives of the whole animal, and it would be difficult to see it with the magnifying power likely to be used for making such a drawing, while in the view of the uropoda from beneath, which is the one shown in Dana's enlarged figure, it is quite concealed. In other respects it agrees so well with Dana's description and figure that I identify it without much hesitation with his species.

It can be readily distinguished from *A. danæ*, Heller, which it otherwise greatly resembles, by the absence of a groove on the inferior margin of the first segment of the



mesosome. The specimens from Nelson, Wellington, &c., previously identified with this species by Mr. Thomson and myself \*, do not belong to this species, but to *Armadillo ambitiosus*, Budde-Lund.

4. *ARMADILLO RUGULOSUS*, Miers, 1876. (Pl. 16. fig. 7.)

*Cubaris rugulosus*, Miers, Ann. & Mag. Nat. Hist. ser. 4, xvii. p. 225 (1876); Cat. N. Z. Crust. p. 96, pl. ii. fig. 5 (1876).

*Cubaris rugulosus*, Chilton, Trans. N. Z. Inst. xv. p. 73 (1882).

*Armadillo rugulosus*, Budde-Lund, Isopoda Terrestria, p. 40 (1885).

*Cubaris rugulosus*, Filhol, Mission de l'île Campbell, p. 440 (1885).

*Cubaris rugulosus*, Thomson & Chilton, Trans. N. Z. Inst. xviii. p. 158 (1888).

*Specific description*.—Body moderately convex, surface of segments uneven, faintly rugose. Head broad and transverse, front margin revolute, first segment of mesosome with two shallow depressions diverging anteriorly on the anterior part of the upper surface; posterior margin sinuous, angles produced backwards; lower posterior margin with a notch for reception of succeeding segment, the notch not extending along the inferior margin; second segment similarly notched. Dorsal surface of segments of mesosome often with a slight groove parallel to posterior margin; the second, third, and fourth narrowed at sides with inferior margins rounded; fifth, sixth, and seventh broader, with inferior margins truncate. Metasome with terminal segment broadest at base, sides at first suddenly converging, then parallel or slightly divergent, extremity square truncate. Antennæ finely hirsute, flagellum shorter than fifth joint of peduncle, second joint three times as long as the first. Uropoda with outer branch small, not quite reaching to the end of last segment; inner branch short, reaching half way from its base to end of last segment.

*Colour* light brown, with variegated markings of a rich reddish brown, some specimens very dark.

*Length* about 6 mm.

*Habitat*.—Very abundant in South Island.

*Remarks*.—This species is much smaller than either of the two preceding, and may generally be readily distinguished from them by the different character of the notches in the posterior lateral margins of the first and second segments of mesosome. I have, however, some specimens from Kenepuru in which these notches are less marked, and the inner branch of the uropoda is a little longer than usual, and the colour is rather greyish. The specimens are not very well preserved, and I prefer for the meantime to consider them merely as a variety of the species under consideration.

The oblique depressions on the first segment of the metasome described by Miers are generally present, but are more distinct in some specimens than in others; they are also present in some specimens of *Armadillo ambitiosus*, Budde-Lund, and are probably more or less the necessary consequence of the head fitting in to the first segment when the animal is rolled up, and are therefore probably of little classificatory value. In some specimens the irregularities on the dorsal surface are more distinct than in others, and

\* Trans. N. Z. Inst. xviii. p. 159.

they may even give the appearance of a poorly-marked transverse row of small tubercles on the segments of the metasome; it is perhaps specimens of this kind that Heller described under the name *Spherillo monolinus*, but as he says nothing about the notches on the inferior margins of the first two segments of the metasome, I do not feel justified in definitely identifying our species with his.

5. *ARMADILLO MONOLINUS*, Dana, 1853.

*Spherillo monolinus*, Dana, U. S. Explor. Exped., Crust. ii. p. 719, pl. 47, fig. 3 (1853).

*Spherillo monolinus*, Heller, Voy. Novara, Crust. p. 135 (1865).

*Armadillo Aucklandicus*, Budde-Lund, Isopoda Terrestria, p. 40 (1885).

I have seen no specimens that I could refer to this species. Dana describes it as follows:—

“Head arcuate in front. Segments of thorax transversely marked with a beaded ridge and laterally truncate, anterior segment longest and marked with two beaded ridges. Abdomen semicircular, third, fourth, and fifth segments laterally obtuse, the last with a nearly subquadrate apex, and much broader at base. Caudal appendages subtriangular, shorter than breadth at base, inner margin broadly excavate. Antennæ nearly naked, flagellum hardly shorter than preceding joint. Length 4 lines.”

Dana's specimens were obtained at “Wykare River, near Bay of Islands.”

Heller describes a specimen from Auckland, and at the end of his description says: “I denote this species as *S. monolinus*,” without making it clear whether he is referring it to Dana's species or giving it as a new species, using by inadvertence the same name. Budde-Lund supposes Heller's species to be new, and therefore changes the name to *Aucklandicus*. I think, however, that it is more likely that Heller intended to refer his specimen to Dana's species, and there is nothing in his description inconsistent with this supposition; Miers had evidently taken this to be Heller's intention, but curiously enough he does not give the reference to Heller's description, though he quotes it for the habitat when describing *Spherillo monolinus*, Dana. It is possible that this species may be the same as *A. rugulosus*, Miers.

6. *ARMADILLO HAMILTONI*, sp. nov.

“Remarkably sculptured Terrestrial Isopod.”—G. M. Thompson, Annals & Mag. N. H. ser. 6, xii. p. 225, pl. iv.

*Specific description*.—Oblong-oval, breadth rather more than half the length, epimeral portions greatly developed and projecting downwards and outwards, central part greatly raised above the epimera and richly supplied with spines and crests. Cephalon with the dorsal surface produced forwards into a thin plate projecting far over the bases of the antennæ; from the dorsal surface of the cephalon arise two transverse lateral crests or flanges, which project horizontally forwards as far as the central prolongation of the vertex; the posterior margin of the cephalon is curved upwards, and a little exterior to the median line is produced upwards into a conical tooth; the posterior margins of each segment of the mesosome is similarly produced upwards and somewhat backwards into two teeth, those on the seventh segment being very large and prominent; the first

segment has two pairs, and each of the other six segments one pair, of conical teeth or spines arising at right angles to the dorsal surface and situated in the same longitudinal lines as the teeth already described. More laterally each of the first six segments bears on each side two thin crests arranged in two longitudinal lines, but the crests of each segment widely separated from those of the contiguous segments; in the seventh segment the outer pair of crests is represented only by small spines. External to the outer row of crests each segment bears two or three small tubercles or spines, which are concealed in dorsal view by the outer row of crests. Epimera very largely developed and projecting somewhat horizontally, that of the first segment much larger than any of the others; first two segments of metasome concealed in dorsal view by the projecting hinder margin of the last segment of the mesosome; each of the third to fifth segments has the hinder margin produced into two teeth similar to those in the mesosome but smaller; these teeth increase in size from the third to fifth segment. From the centre of the terminal segment arises a small keel projecting backwards, and ending in a sharp tooth; the epimera of the third to fifth segments are very long and narrow; hinder margin of terminal segment straight, not much narrower than the base; sides concave.

Eyes of moderate size, convex, of about twenty facets. Antennulæ and antennæ not observed. Uropoda with the lateral portion of the joint long and narrow, end rounded, outer branch narrow, fully three times as long as broad, arising from a well-marked notch in the inner margin of the base, not reaching to the end of the terminal segment, ending in a small seta; inner branch very short, scarcely reaching as far as the base of the outer branch.

*Colour* a rich brown, with numerous markings of a darker brown.

*Length* 6 mm.

*Habitat*.—Petane, near Napier (*A. Hamilton*).

*Remarks*.—In accordance with a wish expressed by Mr. G. M. Thomson, I gladly name this species after its discoverer, Mr. A. Hamilton. I have only the dried specimen originally described and figured, but not named, by Mr. Thomson, but it is, I think, sufficient to show that the species may, provisionally at any rate, be placed under *Armadillo*. The wealth of crests and spines or teeth on the dorsal surface is quite extraordinary, and I fear that the description will convey a very inadequate idea of the actual specimen; a better idea may be got by consulting Mr. Thomson's figures. Mr. Thomson describes the legs as "very feebly developed and, as far as I could make out, appear to want the dactylos." There are no legs now attached to the specimen, but in the tube I found two fragments possessing normal dactyla similar to those found in other species of *Armadillo*.

#### 7. *ARMADILLO MACMAHONI*, sp. nov. (Pl. 16. fig. 8.)

*Specific description*.—Body convex, tuberculated and setose, especially on the tubercles; surface with depressed hexagonal markings. Cephalon with the dorsal surface roughened, somewhat setose, front with well-marked transverse ridge, a little lower in the middle. First segment of mesosome with inferior margin revolute anteriorly, posterior portion deeply notched, second segment also notched, but with the inner lip of the notch not

reaching downwards so far as lower margin. The mesosome bears four longitudinal rows of tubercles (*i. e.*, from tubercles on each segment), the two inner rows a little external to the median line, the other two more lateral; on the anterior segments the tubercles are not very prominent, but on the succeeding segments they become larger and more prominent and project slightly backwards; on the seventh segment the two median tubercles are very large and project backwards over the metasome, while the lateral tubercles are poorly marked and form only slight elevations at the outer side of the base of the others. The tubercles are covered especially near the apex with numerous stiff setæ. Shorter setæ are also found on the rest of the surface, and some of them, especially along the posterior margins of the segments, are broad and scale-like. Metasome with an indistinct median ridge formed by a setose tubercle on each of the last four segments, that on the fifth the largest; first and second segments short, the first almost concealed by the preceding segment, all the segments of mesosome fitting closely together; terminal segment much broader than long, sides concave, posterior margin slightly convex.

Eyes rather small, of about ten ocelli. Antennæ short.

Uropoda with base fitting closely into the space between the side-plates of the fifth segment and the terminal segment; outer branch very minute, not projecting beyond the inner margin of the base, inner branch reaching about to end of last segment.

Colour brown.

Length about 6 mm.

*Habitat*.—Kenepuru, Marlborough, in the bush (*MacMahon*).

*Remarks*.—I take pleasure in naming this fine species after Mr. Joseph MacMahon, to whom I am indebted for many Terrestrial Isopoda collected at Kenepuru.

#### 8. ARMADILLO SPINOSUS, Dana, 1853.

*Spherillo spinosus*, Dana, U. S. Explor. Exped., Crust. ii. p. 723, pl. 47, fig. 6 (1853).

*Spherillo spinosus*, Miers, Cat. N. Z. Crust. p. 97 (1876).

*Armadillo spinosus*, Budde-Lund, Isopoda Terrestria, p. (1885).

*Spherillo spinosus*, Thomson & Chilton, Trans. N. Z. Inst. xviii. p. 159 (1885).

The following is Dana's description of this species:—

"Body bristled throughout with subacute spines, margin either side a little produced and segments laterally truncate. Head nearly trapezial, arcuate in front, and a little broader than behind. First segment of thorax largest; segments of abdomen laterally obtuse, the last subquadrate, not broader at base, truncate at apex.

"New Zealand, near Bay of Islands (Coll. Dr. C. Pickering; *Dana*). Under bark of pine-trees."

*Remarks*.—I have seen no specimens of this species, but it appears to come near *A. MacMahoni*, differing, however, in having the spines much more numerous and more acute.

## EXPLANATION OF THE PLATES.

*Reference Letters.*

- $a^1$  = antennula.  
 $a^2$  = antenna.  
 $c$  = cephalon.  
 $l.s.$  = labrum superior.  
 $l.i.$  = labrum inferior.  
 $M.dex.$  = right mandible.  
 $M.sin.$  = left mandible.  
 $mx^1$  &  $mx^2$  = 1st and 2nd maxillæ.  
 $mxp.$  = maxillipede (outer, *i. e.*, posterior or under aspect).  
 $mxp^*$  = maxillipede (inner, *i. e.*, anterior or upper aspect).  
 $prn$  = percion (or mesosome).  
 $p^{1,2 \dots 7}$  = 1st, 2nd, 3rd . . . 7th leg.  
 $p^1$ , &c. = extremity of 1st leg, &c.  
 $pl$  = pleon (or metasome).  
 $plp^{1,2}$ , &c. = 1st, 2nd pleopod (anterior aspect).  
 $plp^{1,an.}$ , &c. = 1st pleopod, &c. (posterior aspect).  
 $urp$  = uropod.

[Where necessary, the sex is indicated by the sign ♂ or ♀ placed after the letters as above.]

## PLATE XI.

Fig. 1. *Ligia novæ-zealandiæ*, Dana. Dorsal view of whole animal and details.

## PLATE XII.

Fig. 1. *Trichoniscus phormianus*, sp. nov. Dorsal view and details.

2. *Trichoniscus otakensis*, sp. nov. Dorsal and side views of female, dorsal view of male, and enlarged view of head and antennæ of female.

3. *Haplophthalmus Helmsii*, sp. nov. Dorsal view and details.

## PLATE XIII.

Fig. 1. *Trichoniscus Thomsoni*, Chilton. Dorsal view and details.

2. *Tylos neozelandicus*, sp. nov. Side view and details.

## PLATE XIV.

Fig. 1. *Scyphoniscus waitatensis*, nov. gen. et sp. Dorsal view and details.

2. *Scyphax ornatus*, Dana. Dorsal view and details.

PLATE XV.

- Fig. 1. *Scyphax ornatus*, Dana (continued). Details.  
 2. *Scyphax* (?) *aucklandiae*, G. M. Thomson. Dorsal view and details.  
 3. *Actæcia euchroa*, Dana. Dorsal view and details.  
 4. *Actæcia opihensis*, sp. nov. Dorsal view of pleon and details.

PLATE XVI.

- Fig. 1. *Actæcia opihensis*, sp. nov. (continued). Details.  
 2. *Oniscus punctatus*, G. M. Thomson. Details.  
 3. *Oniscus kenepurensis*, sp. nov. Dorsal view and details.  
 4. *Philoscia pubescens*, Dana. Details.  
 5. *Armadillo ambitiosus*, Budde-Lund. Antenna and terminal portion of pleon.  
 6. *Armadillo speciosus*, Dana. Terminal portion of pleon.  
 7. *Armadillo rugulosus*, Miers. View from below of lower margins of 1st and 2nd segments of pereion.  
 8. *Armadillo Macmahoni*, sp. nov. Dorsal and side views and dorsal view of pleon and details.



# TERRESTRIAL ISOPODA OF NEW ZEALAND.

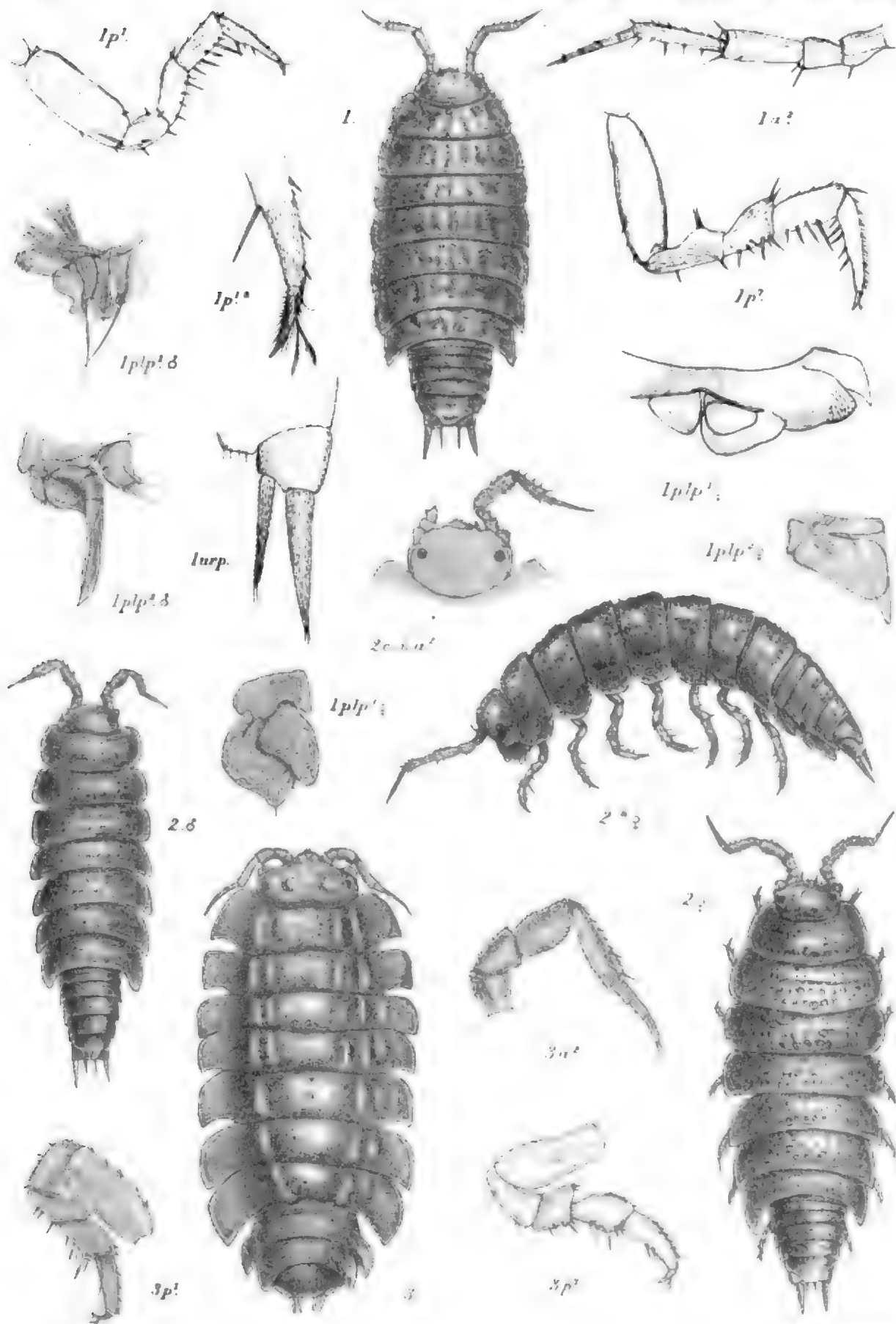
(TRANS. LINN. Soc., 2nd ser. Zool. vol. viii. pt. 4.)

## ERRATA.

- Page 103, line 7 from top, delete the comma after "portion."
- " " " 5 from bottom, insert a comma after "lamellar."
- " 104, " 17 from top, for "Glomeridæ" read "Glomeridæ."
- " 105, " 4 " for "with" read "without."
- " 114, " 17 " for "eggs" read "eyes."
- " 122, " 10 " for "Hayer" read "Harger."
- " 123, " 27 " for "Hayer" read "Harger."
- " " " 35 " for "occasionally" read "provisionally."
- " 126, " 22 " for "rein" read "view."
- " 127, " 9 " for "but with apex" read "both with apex."
- " 130, " 26 " for "Hayer" read "Harger."
- " " " 34 " for "eggs" read "eyes."
- " " between lines 3 & 4 from bottom insert :—
- " " *Cylloma oculatum*, Budde-Land, Isopoda Terrestria, p. 46 (1885)."
- " 131, line 11 from bottom, for "extremities" read "antennulæ."
- " 138, " 14 from top, for "p. 144" read "p. 444."
- " 145, " 14 " for "last segment" read "uropoda."
- " 148, " 2 " for "metasome" read "mesosome."
- " 151, " 18 " for "plp<sup>1.22</sup>, &c." read "plp<sup>1.22</sup>, &c."







'has' 'alten de'.

A. J. Nathan, <sup>1</sup> London









PLATE 10



Illustration of the insects of the genus.



V. *Étude d'une Espèce nouvelle de Lépadides* (*Scalpellum giganteum*, n. sp.) et de *Pœcilasma carinatum*, Hoek. Par Monsieur A. GRUVEL, Chargé d'un Cours de Zoologie à la Faculté des Sciences de Bordeaux. (Communiqué par M. le Professeur HOWES, Sec. Linn. Soc.)

(Planche 17.)

Lu le 21 février, 1901.

JE dois à la haute bienveillance de Monsieur le Professeur Ray Lankester, Directeur du British Museum (Nat. Hist.), et à l'amabilité de son collaborateur, Monsieur Jeffrey Bell, de pouvoir décrire aujourd'hui la plus grande espèce actuellement connue appartenant au genre *Scalpellum*. C'est à cause de ses dimensions relativement considérables que je propose de lui donner le nom de *Sc. giganteum*.

Sur le pédoncule de l'un des échantillons, se trouvait fixé un *Pœcilasma* que l'étude m'a démontré être *P. carinatum*, décrit par Hoek, dans son "Report on the Cirripedia" du 'Challenger.' La comparaison que j'en ai pu faire avec les échantillons types de Hoek au British Museum, ne m'ont laissé aucun doute à cet égard. Je reviendrai du reste plus loin sur quelques-uns des caractères de cette espèce.

*SCALPELLUM GIGANTEUM*, n. sp. (Planche 17. fig. 1.)

*Diagnose*.—Quatorze plaques capitulaires, entièrement calcifiées, recouvertes, presque complètement, par une épaisse cuticule chitineuse, l'apex seul faisant saillie en dehors. Limite exacte des plaques impossible à déterminer sans enlever la cuticule; ces plaques sont largement séparées les unes des autres. Capitulum aplati surtout vers le sommet, carène régulièrement courbe, *umbo* à l'apex. *Umbo* des plaques caréno-latérales très rapproché de la base, recourbé en avant et n'atteignant pas le bord externe de la carène. Rostre ovale, entièrement caché sous la cuticule.

Pédoncule aussi long que le capitulum, à peu près régulièrement cylindrique, orné de six séries longitudinales et alternes, d'écailles allongées transversalement, non imbriquées, chaque rangée longitudinale comprenant de 10 à 12 écailles recouvertes par la cuticule.

Dimensions :—Longueur du capitulum, 45 mm. ; largeur, 32 mm.

Longueur du pédoncule, 45 mm. ; largeur, 15 mm.

Cette espèce est voisine de *Sc. regium*, Hoek, et *Sc. Darwinii*, Hoek, mais elle s'en distingue nettement par un certain nombre de caractères et en particulier la forme des plaques et des écailles.

Je l'ai désignée sous le nom de *Sc. giganteum*, car c'est la plus grande espèce actuellement connue.

*Capitulum*.—Le capitulum est aplati, beaucoup plus vers le sommet que vers la base. Vu par le côté, il représente un triangle curviligne, presque isocèle (le côté dorsal étant cependant un peu plus long que le côté ventral), dont les deux côtés seraient convexes et la

base légèrement concave. Le bord antérieur forme une ligne à peu près régulièrement convexe.

Les quatorze plaques qu'il porte sont largement séparées les unes des autres, surtout les principales, et noyées dans une épaisse cuticule chitineuse jaunâtre sale, un peu comme chez *Sc. squamuliferum*, Weltner, mais la cuticule a ici une épaisseur bien plus considérable. Il est impossible de se rendre un compte exact de la forme et de la disposition de ces plaques si on n'enlève pas, au préalable, la plus grande partie de la cuticule qui les recouvre et qui, se poursuivant entre elles, sert à les unir les unes aux autres.

Les stries d'accroissement des plaques sont, du reste, parfaitement nettes sur la cuticule. Celle-ci est couverte de nombreux poils courts fortement barbelés, de petites verrues chitineuses couvertes de poils très courts et enfin par de nombreux tubercules chitineux, plus fortement colorés que le reste de la cuticule et disséminés d'une façon assez dense mais irrégulièrement. Le tout produit au doigt, quand on le passe sur le capitulum, la sensation qu'on éprouve en passant le doigt sur un velours un peu raide.

La cuticule se poursuit, du reste, sur le pédoncule, sans modification appréciable dans sa structure.

*Tergum*.—Forme irrégulièrement quadrangulaire. Bord antérieur convexe; bord scutal convexe dans sa partie inférieure, concave dans sa partie supérieure et terminé antérieurement par un très court espace rectiligne. Bord carénal droit et bord caréno-apical légèrement concave, ce qui fait que l'apex qui est droit, semble, cependant, légèrement recourbé en arrière. Une arête nette unit l'apex à l'angle inférieur, les stries d'accroissement sont nettement visibles. (Pl. 17. fig. 2.)

*Scutum*.—A peu près triangulaire, bord antérieur convexe, bord inférieur très légèrement convexe aussi, enfin bord latéro-tergal convexe sur ses  $\frac{2}{3}$  inférieurs et concave sur son  $\frac{1}{3}$  supérieur, ce qui fait que l'apex qui est droit, semble aussi légèrement recourbé en arrière.

La longueur du bord inférieur n'égale pas la  $\frac{1}{2}$  de celle du bord antérieur. Une arête nette va de l'apex à l'angle inféro-interne; stries d'accroissement bien marquées. (Pl. 17. fig. 2.)

*Carène*.—Régulièrement courbe; umbo à l'apex qui ne fait pas saillie entre les terga. Bord dorsal convexe, ainsi que les bords latéraux. Le bord basal est fortement convexe et son angle inférieur, mousse, n'atteint pas le sommet des pièces caréno-latérales. Concave à sa partie interne, elle va en s'élargissant régulièrement du sommet vers la base. (Fig. 2.)

*Plaque latérale supérieure*.—Irrégulièrement quadrilatère; bord tergal droit, bord scutal fortement excavé, ce qui fait saillir l'apex en avant; les bords postérieur et inférieur sont régulièrement courbe et se coupent à angle très arrondi. (Fig. 2.)

*Rostre*.—Petit et ovale; bords latéraux cachés par le sommet et les bords internes très concaves des pièces rostro-latérales. Il est, du reste, entièrement masqué par la cuticule.

*Plaque rostro-latérale*.—Allongée, étroite, plus large dans sa partie antérieure que dans sa partie postérieure. Le bord rostral est concave et délimite, avec son congénère, un espace ovale où se place la partie centrale du rostre. Cette pièce rostro-latérale est inclinée en avant.

*Plaque infra-médio latérale.*—De forme triangulaire ; le bord inférieur est le plus long, puis le bord postérieur et enfin le bord antérieur. Apex dirigé vers le sommet du capitulum.

*Plaque caréno-latérale.*—Allongée, étroite, inclinée en arrière. Apex fortement recourbé en haut et en avant et n'atteignant pas le bord inférieur ni le bord externe de la carène. Umbo très rapproché de la base. Le bord inféro-dorsal est arrondi et égal environ à une fois et demi la longueur du bord supérieur. Quant au bord carénal, il est très concave et sa longueur dépasse un peu la moitié de celle du bord supérieur.

Les limites de la chitine qui borde les plaques ne correspondent pas du tout comme forme et comme disposition à celles des plaques elles-mêmes. Cette limite est, du reste, pour les plaques inférieures, très difficile à déterminer. Les descriptions que nous venons de donner portent sur les pièces calcaires seulement, telles qu'on les aperçoit après avoir enlevé la chitine qui les recouvre (fig. 2). Dans la fig. 1 les animaux sont représentés tels qu'on les trouve, c'est à dire entièrement recouverts par la chitine.

Longueur du capitulum, 45 mm. ; largeur, 32 mm. ; épaisseur max., 16 mm.

*Pédoncule.*—Aussi long que le capitulum et presque aussi large. De forme à peu près régulièrement cylindrique, mais cependant légèrement dilatée vers le capitulum et vers la base. Il est orné de six séries longitudinales et alternes d'écailles allongées transversalement, non imbriquées et séparées, d'une série à l'autre, par un espace chitineux assez large, chaque série longitudinale comptant de 10 à 12 écailles en général entièrement recouvertes par la cuticule, mais quelques unes ont leur bord libre érodé et mis à nu. L'écaille apparaît alors, très blanche.

Longueur du pédoncule, 45 mm. ; largeur, 15 mm.

*Bouche.*—Le *labre* est fortement saillant en avant (*lab*, figs. 7 et 8). Vu de face, il a un peu la forme d'une coupe ; la partie antérieure est arrondie et se trouve séparée par un rétrécissement de la partie postérieure écrasée ; le bord postérieur est échancré en son milieu pour recevoir les extrémités des autres pièces masticatrices. Ce bord ne porte, du reste, aucune espèce d'ornements.

Les *Palpes* (fig. 3) sont aplatis en lames et ornés vers les extrémités libres et les parties supérieure et inférieure de soies assez courtes et fortement barbelées. L'épithélium est chargé de nombreuses cellules pigmentaires d'un brun noir et disposées avec assez de régularité.

Les *Mandibules* (fig. 4) portent trois dents, dont la supérieure est la plus longue et la plus forte ; elle est un peu plus éloignée de la deuxième que celle-ci de la troisième.

L'angle inférieur est saillant et garni de soies courtes et robustes ; les plus longues sont situés à l'extrémité.

Les *Mâchoires* (fig. 5) présentent une forte dent supérieure, suivie de nombreuses dents, formant une dizaine de rangées de plus en plus courtes et faibles. Entre celles-ci s'en trouvent d'autres fines et non rigides. Il n'existe pas d'encoche sur le bord libre, qui est d'abord légèrement concave dans sa moitié supérieure, mis légèrement convexe dans sa moitié inférieure. Le bord supérieur des pièces porte des soies longues et flexibles. Aucune n'est barbelée.



Enfin les *Palpes* de la lèvre inférieure (fig. 6) sont les pièces les plus larges de l'appareil masticateur. Leur bord libre présente une légère encoche en son milieu et cette encoche détermine ainsi la formation d'une saillie supérieure et d'une inférieure, portant chacune une touffe de soies, barbelées d'une façon identique à celle des soies des palpes de la lèvre supérieure. Sur le bord supérieur, il existe aussi des soies beaucoup plus longues, plus fines, et également irrégulières et barbelées.

*Cirrhes*.—Les cirrhes sont, en général, assez longs et robustes.

1<sup>re</sup> paire : Rames inégales, l'antérieure avec 12 articles ; c'est le 4<sup>e</sup> à partir de la base qui atteint le maximum de largeur. Ils sont garnis de soies nombreuses et assez courtes sur toute la surface interne et sur les bords antérieur et postérieur.

La rame postérieure porte 16 articles, et la région moyenne, qui est la plus large, a une largeur égale, environ, à la moitié de celle du 4<sup>e</sup> article de la 1<sup>re</sup> rame. Les soies sont disposés de la même façon.

La 2<sup>e</sup> paire est légèrement séparée de la 1<sup>re</sup>. Les rames sont à peu près égales, cependant la postérieure dépasse l'antérieure des 4 derniers articles extrêmement courts. La rame antérieure porte 31 articles.

Les 3<sup>e</sup>, 4<sup>e</sup> et 5<sup>e</sup> paires de cirrhes sont semblables à la 2<sup>e</sup>.

Quant à la 6<sup>e</sup> paire : la rame postérieure, qui possède 48 articles et a 50 mm. de long., dépasse l'antérieure des deux derniers. Les soies qui les garnissent antérieurement sont longues, robustes et terminées en pointe très fine à l'extrémité ; elles sont disposées en 4 doubles rangées vers les articles terminaux. Postérieurement, à la limite des articles, se trouvent groupées 5 ou 6 soies courtes.

*Appendices caudaux*.—Formés chacun de 4 articles, dont le basilaire égale en longueur les 3 autres. Les articles vont en s'élargissant vers l'extrémité libre, de sorte que le dernier est le plus large et sa partie distale est, elle-même, plus large que sa base, de plus elle est nettement tronquée (fig. 8'). A la limite des articles, du côté interne et du côté externe, se trouvent des groupes de soies dont les plus longues sont celles de l'article terminal, et leur longueur ne dépasse pas celle de cet article lui-même.

*Pénis*.—Rétréci et recourbé à sa base, il reste à peu près cylindrique sur la moitié de sa longueur. A partir de là, il s'amincit progressivement pour se terminer en pointe fine, mousse et ornée d'un petit bouquet de soies, soies que l'on retrouve disséminées sur sa moitié terminale, irrégulièrement disposées. La longueur du pénis, après séjour dans l'alcool, est de 12½ mm.

Sur les cinq échantillons que j'ai eus à ma disposition, il m'a été impossible de découvrir la moindre trace de mâles dits *complémentaires*.

Cette superbe espèce, ressemble un peu extérieurement et seulement en ce qui concerne le capitulum à *Sc. squamuliferum*, Weltner, mais elle a des affinités bien plus grandes avec *Sc. regium*, Hoek, et *Sc. Darwinii*, Hoek, cependant les seuls caractères des plaques capitulaires et des écailles pédonculaires suffisent à les différencier nettement—ainsi que j'ai pu m'en rendre compte par l'étude des échantillons mêmes du 'Challenger.'

*Localité*.—Côtes de Cuba, par cinq cents brasses de fond. British Museum.

**PÆCILASMA CARINATUM, Hoek.\***

J'ai dit, au début de ce travail, que j'ai rencontré sur le pédoncule de l'un des échantillons de *Scalpellum giganteum*, A. Gruvel, un *Pæcilasma* que j'ai reconnu être *P. carinatum*, Hoek. Ceci m'a amené à faire une étude complète de cette espèce que je vais rapporter ici, afin de compléter quelques points laissés un peu dans l'ombre par Hoek. J'y ajouterai quelques dessins, car il me paraît nécessaire de représenter l'aspect des animaux que l'on étudie avec une scrupuleuse exactitude. Les descriptions, aussi bien faites soient-elles, présentent toujours une élasticité d'interprétation que n'offre pas le dessin ; l'exactitude des unes et de l'autre constituent donc une condition nécessaire et indispensable pour permettre aux classificateurs, même les plus scrupuleux, qui viennent ensuite, de commettre des erreurs involontaires et de les exposer à nommer des espèces une seconde fois.

**Diagnose.**—Cinq plaques capitulaires. Carène considérablement élargie à sa partie inférieure et terminée en un disque plein sans fourche différenciée. Dents umbonales du scutum très peu fortes ; bord caréno-tergal du scutum échancré vers son tiers inférieur pour recevoir les parties latérales du disque de la carène. Angle inférieur des terga tronqué et à bord carénal sensiblement parallèle au bord occluseur. Pédoncule court, atteignant seulement le  $\frac{1}{3}$  de la longueur du capitulum, sans ornements nets.

Mandibules non semblables, trois dents à gauche et quatre à droite. Appendices caudaux uniarticulés et de longueur égalant à peu près le  $\frac{1}{4}$  ou le  $\frac{1}{5}$  de la longueur du pédicelle de la 6<sup>e</sup> paire de cirrhes.

Dimensions du plus grand échantillon étudié :—

Longueur du capitulum, 14 mm. ; largeur,  $4\frac{1}{2}$  mm. ; maximum d'épaisseur, 4 mm.

Longueur du pédoncule,  $2\frac{1}{2}$  mm. ; largeur, 2 mm.

**Habitat.**—Côtes de Cuba, par un fond de 500 brasses. Collection du British Museum.

**Capitulum.**—Le capitulum étant environ trois fois aussi long que large, il en résulte qu'il présente une forme élancée bien plus accentuée que ne le représente le dessin de Hoek. Il est comprimé latéralement vers sa région supérieure, tandis que le maximum d'épaisseur se trouve vers le quart inférieur environ. Il est orné de cinq plaques d'un blanc-crème, ne laissant entre elles aucun espace libre. Elles sont recouvertes par une très mince cuticule, sans autres ornements que quelques rares poils irrégulièrement disséminés. On aperçoit sur les plaques des striations très fines mais cependant nettes.

**Terga.**—Les terga sont relativement très peu développés ; l'apex est terminé en pointe, le bord antérieur droit, l'angle basal tronqué, le bord adjacent à la carène étant sensiblement parallèle au bord occluseur, mais la saillie de l'angle inférieur du tergum vers le scutum est beaucoup moins marquée que ne le figure Hoek.

**Scuta.**—Très développés par rapport aux autres plaques, mais non divisés en deux. Ils sont renflés vers le tiers inférieur et surtout dans la région antérieure. Le bord antérieur ou occluseur est fortement saillant en avant, particulièrement vers son tiers

\* Hoek, Report on the Cirripedia. Voyage of 'Challenger,' 1883.

supérieur, mais il est cependant, à peu près régulièrement courbe. Le bord tergal est droit. Le bord basal très étroit, à peu près comme le bord basal de la carène qui lui est adjacent et qui forme avec le premier une ligne légèrement concave inférieurement, entourant le sommet du pédoncule qui semble ainsi légèrement détaché du capitulum dans cette partie proximale. La particularité la plus caractéristique c'est que le bord carénal forme, dans son tiers inférieur, une concavité destinée à loger les bords latéraux du disque inférieur de la carène.

Assez fréquemment, on remarque, à la partie inféro-interne des scuta, à une petite distance du bord basal, une ligne circulaire, limitant avec celui-ci, une surface légèrement concave, un peu en saillie et portant des cannelures parallèles formant des denticulations à leur contact avec le bord basal. (Fig. 15.)

A l'umbo de chaque scutum se trouve une dent interne très peu accentuée, mais nette, cependant.

Enfin la convexité des deux plaques scutales est identique.

*Carène.*—La carène est courte. Son apex dépasse de peu le niveau du milieu du bord dorsal du capitulum. La partie supérieure est beaucoup plus étroite que l'inférieure, mais le minimum de largeur se trouve un peu au-dessus du disque basal. L'arête dorsale est saillante.

La carène se dilate inférieurement pour former deux expansions aplaties, à bord libre arrondi et allant, chacune, se placer dans une cavité correspondante des scuta.

Vu du côté interne, il faut se représenter ce disque, comme une sorte de trapèze isocèle, plié en son milieu et séparé du reste de la carène par un bord légèrement concave et en relief (fig. 14). Dans ses régions médiane et latérales, cette partie du disque présente une surface ressemblant aussi à un trapèze isocèle, à côtés à peu près parallèles à ceux du premier et entièrement en saillie sur la première surface. En son milieu, elle se prolonge inférieurement en une pointe mousse. Cette pointe, qui n'est pas figurée par Hoek, semble cependant normale.

Extérieurement, de chaque côté de l'arête dorsale, les lames du disque présentent parfois des cannelures parallèles, formant sur le bord basal des denticulations. La présence de ces cannelures concorde avec celle des mêmes ornements des scuta (fig. 16).

*Pédoncule.*—Le pédoncule ne dépasse pas en longueur le  $\frac{1}{2}$  de celle du capitulum. Il ne présente aucune trace d'annulation régulière et la cuticule qui le recouvre est simplement ornée par quelques poils courts et irréguliers.

*Bouche.*—Le *Labre* porte, sur son bord libre, quelques dents faibles et courtes.

Les *Palpes de la lèvre supérieure* sont allongés, subconiques, avec quelques soies longues et fines sur leur bord dorsal et d'autres plus courtes et plus raides vers leur extrémité libre.

Les *Mandibules* sont bien exactement celles décrites par Hoek, c'est à dire que la mandibule *gauche* ne présente que *trois* dents, la troisième formant deux pointes saillantes entre lesquelles s'en trouvent de plus petites, tandis que la *droite* porte *quatre* dents, la quatrième étant également bilobée, avec des pointes intermédiaires moins accentuées. Ce ne serait donc pas là une anomalie, comme Hoek était en droit de le supposer,

mais bien une atrophie acquise définitivement. Quant à ce qui concerne les *Mâchoires*, je n'ai rien à ajouter ni à modifier à la description de Hoek.

Enfin les *Palpes de la lèvre inférieure* sont aplatis, à bords antéro-supérieurs arrondis et portant de longues soies grêles et flexibles.

*Cirrhés*.—D'une façon générale, les cirrhés sont courts et, cependant, restent grêles. La première paire est située à la base du mamelon buccal et se trouve légèrement séparée de la deuxième.

1<sup>re</sup> paire. Rames presque égales; l'antérieure possède 9 articles, la postérieure 10. L'article basilaire est le plus développé en longueur et en largeur. Les soies sont nombreuses, surtout aux extrémités et du côté interne, en avant et en arrière.

2<sup>e</sup> paire. Dans la majorité des cas, les rames sont semblables à droite et à gauche, leur longueur égalant à peu près deux fois celle de la rame postérieure de la 1<sup>re</sup> paire. Celles du même côté sont sensiblement égales avec 15 et 17 ou 18 articles allongés. Mais dans quelques cas, il se produit du côté gauche une atrophie singulière qui porte sur la rame postérieure.

Tandis, en effet, que la rame antérieure est normale, la postérieure est très grêle et plus courte même que celles de la première paire de cirrhés.

Les autres paires de cirrhés sont à peu près identiques à la deuxième paire normale, avec de 15 à 18 articles.

*Appendices caudaux*.—Ils sont cylindriques, uniarticulés et terminés par un bouquet de soies courtes. Leur longueur atteint environ le  $\frac{1}{4}$  ou le  $\frac{1}{3}$  de celle du pédicelle de la 6<sup>e</sup> paire de cirrhés.

*Pénis*.—Le pénis est long et grêle; son extrémité atteint celle des cirrhés de la 6<sup>e</sup> paire après séjour dans l'alcool. Il ne présente aucune trace d'annulation proprement dite et la cuticule qui le recouvre est simplement ornée de quelques poils, disséminés sur sa périphérie et se réunissant à son extrémité en une touffe assez rigide.

*Distribution géographique*.—Pendant la campagne du 'Challenger' nous dit Hoek, cette espèce a été trouvée deux fois. La première fois, ce fut un tout petit échantillon, par une profondeur de 390 brasses à Colubra Island (West Indies); la seconde fois, à l'île de l'Ascension (Océan Atlantique), par 420 brasses de fond, cinq échantillons furent récoltés fixés sur de coraux. L'échantillon trouvé sur les pédoncules de *Scalpellum giganteum* vient des côtes de Cuba. Enfin il existe au British Museum quelques beaux exemplaires de cette même espèce.

Je désirerais, en terminant cette courte étude, dire un mot de la collection du 'Challenger' que j'ai pu examiner tout à loisir pendant mon séjour au British Museum aux vacances dernières.

Avant d'avancer plus loin dans la longue étude du groupe des Cirrhipèdes que j'ai entreprise et que je voudrais tâcher de mener à bien, j'ai pensé qu'un pèlerinage au lieu même où l'illustre Darwin fit les brillantes et patientes recherches qui l'amènèrent à écrire ses beaux volumes de la 'Monographie des Cirrhipèdes,' s'imposait tout d'abord.

Je tenais à voir de près sa collection conservée au British Museum, ainsi que celle de Hock provenant des campagnes du 'Challenger.'

Je pensais, avec raison, que si bien des fois à l'aide d'une description et de dessins, on peut arriver à se faire une idée nette d'une espèce, il se présentait des cas, pour des espèces très voisines, par exemple, où la comparaison des types mêmes s'impose et comme ces types ne sortent pas, généralement, des collections qui ont l'honneur de les posséder, une visite au British Museum devenait indispensable.

Cette visite, je l'ai faite et je puis affirmer, que grâce à la haute bienveillance de M. le Professeur Ray Lankester, Directeur, ainsi qu'à l'amabilité de tous les Professeurs et Assistants avec lesquels j'ai eu des relations, en particulier avec M. J. Bell, que j'ai dérangé bien des fois de son travail, je n'ai pas perdu mon temps. Tout a été mis de la façon la plus libérale à ma disposition, et je ne saurais trop les en remercier ici.

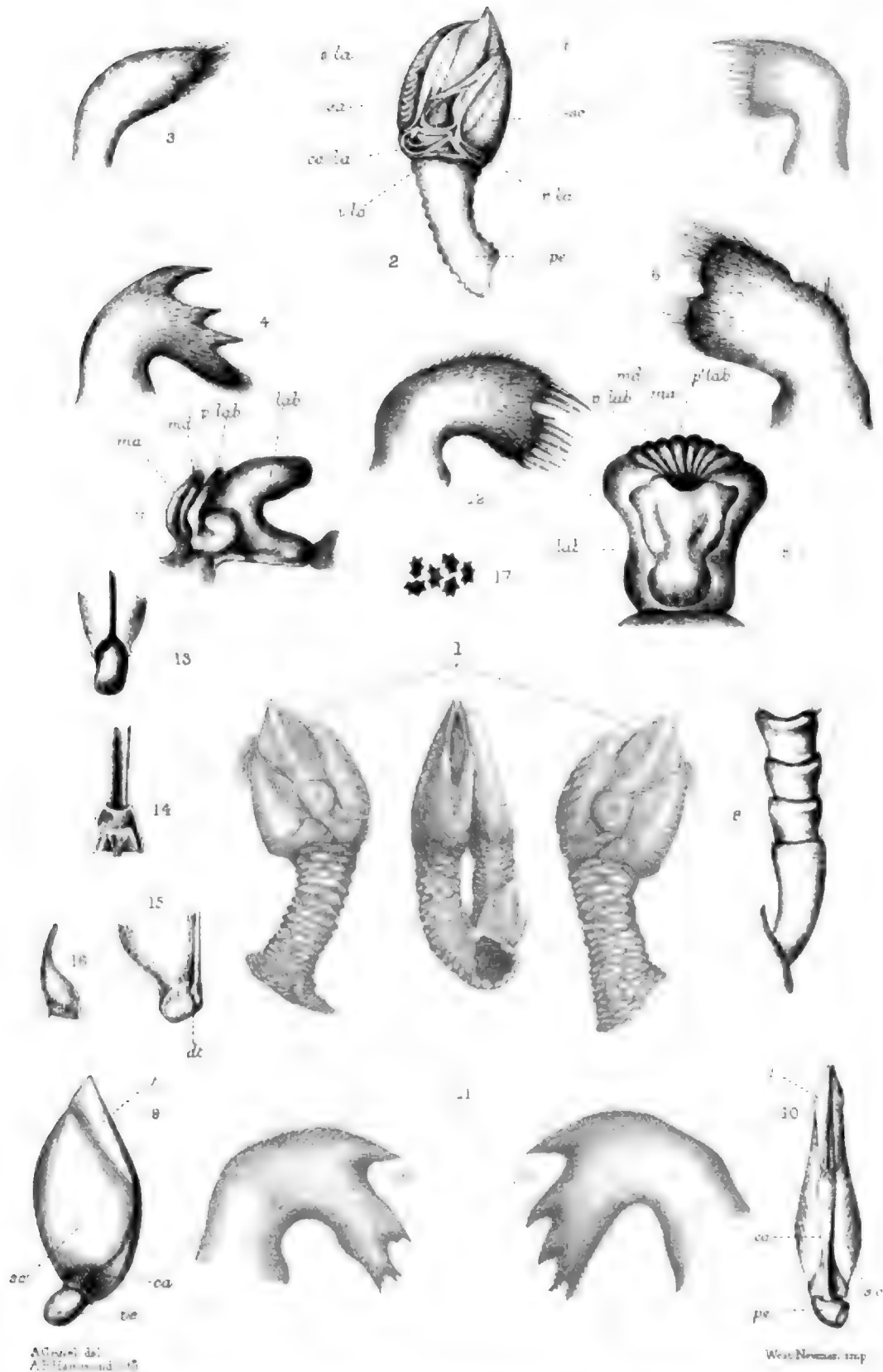
J'ai pu me rendre compte que j'étais dans le vrai en pensant qu'il fallait voir les échantillons eux-mêmes, avant de pouvoir décider en connaissance de cause.

Même quand l'auteur fait lui-même ses dessins, il peut commettre des erreurs, s'il ne les commet pas lui-même, elles proviennent du graveur ou même du tirage. Voilà pourquoi probablement, certains types de Hock sont le plus généralement assez difficilement reconnaissables si l'on s'en rapporte aux dessins qu'il en a donnés. Comme on ne peut pas toujours voir les types, et que les descriptions sont parfois un peu élastiques, même les mieux faites, il en résulte que l'on peut dans ces cas nommer deux fois une espèce, avec la meilleure foi du monde.

En ce qui concerne le genre *Scalpellum*, beaucoup d'espèces, particulièrement celles à plaques imparfaitement calcifiées, ne montrent pas, dans les figures, la limite nette des plaques cependant très visible sur les échantillons.

Cela n'est nullement une critique, mais une simple constatation. Ce sont là surtout des défauts d'édition, mais il n'en est pas moins vrai que cela peut avoir des conséquences assez sérieuses et, toutes les fois que j'en aurai l'occasion, je tâcherai de rectifier ces points obscurs des dessins, en me contraignant, pour être plus exact, à dessiner moi-même à la chambre claire quand cela sera possible ou d'après des documents photographiques, dans les autres cas.

Je crois même que, toutes les fois que la dimension des échantillons le permet, il est bon de remplacer le dessin entièrement par la photographie, comme je l'avais, par exemple, pour la figure 1, représentant un groupe de *Scalpellum giganteum*, mais des difficultés d'exécutions m'ont obligé à remplacer la photographie par de simples dessins. Ce sont là, malheureusement, des difficultés qui se présentent souvent dans l'exécutions des planches et contre lesquelles la meilleure volonté des auteurs est impuissante ! C'est là un fait évident, mais infiniment regrettable, même en se plaçant au point de vue exclusivement scientifique !



A. Gravel del.  
A. Williams sculp.

West Newton, Imp.

1. *POGILASMA GIGANTEUM* n. sp. 2. *POGILASMA CARINATUM* Howe



## EXPLICATION DE LA PLANCHE 17.

[Tous ces dessins ont été faits par l'auteur, soit d'après des photographies, soit à la chambre claire.]

- Fig. 1. *SCALPELLUM GIGANTEUM* dans différentes positions.  
 2. Le même, après qu'une partie de la chitine superficielle a été enlevée pour laisser voir la forme des plaques capitulaires. Le pédoncule est simplement représenté par son contour. *l*, tergum; *sc*, scutum; *ca*, carène; *ca.la.*, plaque caréno-latérale; *r.la*, plaque rostro-latérale; *s.la*, plaque latérale supérieure; *i.la*, plaque infra-latérale; *pe*, pédoncule.  
 3. Palpe de la lèvre supérieure (gauche).  
 4. Mandibule gauche.  
 5. Mâchoire droite.  
 6. Palpe de la lèvre inférieure (droite).  
 7. Mamelon buccal vu de profil. *lab*, labre; *p.lab*, palpe de la lèvre supérieure; *md*, mandibule; *ma*, mâchoire.  
 8. Mamelon buccal vu par la partie supérieure (mêmes lettres).  
 8'. Appendice caudal droit.  
 9. *POECILASMA CARINATUM*, Hoek, vu de profil, dessin à la chambre claire.  
 10. Le même, vu par la face dorsale.  
 11. Mandibules, (*a*) gauche, (*b*) droite.  
 12. Mâchoire gauche.  
 13. Vue de la partie inféro-antérieure de *Poecilasma carinatum*.  
 14. Vue inféro-interne de la carène.  
 15. Scutum gauche, vue inféro-interne; *dt*, dent umbonale interne.  
 16. Carène, vue inféro-externe montrant les cannelures des parties latérales du disque.  
 17. Cellules pigmentaires de l'épithélium de *Sc. giganteum*.

VI. *On the Affinities of *Æluropus melanoleucus*, A. Milne-Edwards.* By E. RAY LANKESTER, M.A., LL.D., F.R.S., F.L.S., Director of the Natural History Departments of the British Museum.

(Plates 18-20.)

Read 21st February, 1901.

SIX years ago my friend the late Professor Alphonse Milne-Edwards, Director of the Jardin des Plantes and Museum of Natural History in Paris, kindly presented to the Oxford University Museum a cast of the skull of the remarkable bear-like animal brought home from Tibet by Père David, and named by him *Ursus melanoleucus*. M. Milne-Edwards in 1875 published a description of this animal and very distinctly stated the conclusion that it must occupy a position intermediate between the Bears (*Ursinae*) and the Panda (*Ælurus*). He formed for it the genus *Æluropus*\*. But subsequently the late Sir W. Flower and Mr. Lydekker in their book, 'Mammals, Living and Extinct,' 1891, whilst dividing the section Arctoidea of the Carnivora into three families,

\* Milne-Edwards' wrote as follows:—"L'ensemble de faits que je viens de passer en revue, prouve que l'Ailoupe ne peut-être rapporté à aucun des types génériques précédemment connus. Il appartient indubitablement à la famille des Carnassiers arctoïdes, dont les Ours sont les principaux représentants, et il ressemble beaucoup à ces animaux; mais il tient encore plus peut-être des Pandas, et il présente un singulier mélange de caractères ostéologiques. Ainsi, par le mode d'articulation de la mâchoire inférieure, l'énorme développement des arcades zygomatiques, il ressemble aux Félines les plus robustes, et quelques naturalistes le comparent à l'Hyène; mais la conformation de ses dents machelières indique que c'est en réalité un animal moins carnivore que ne le sont les Ours. . . . Par la disposition de la couronne, la penultième molaire a beaucoup d'analogie avec les molaires de divers Pachydermes fossiles, notamment des *Charopotamus parisiensis*. . . . Néanmoins c'est entre les Ours et les Pandas que l'Ailoupe doit prendre place dans nos classifications méthodiques, et la division qui le renferme ne paraît avoir une valeur zoologique plus considérable que celle de la plupart des genres dont se compose l'ordre des Carnassiers."

From this it appears that Professor Milne-Edwards regarded *Æluropus* as intermediate between the Bears and the Panda, and therefore probably the representative of a distinct family, although this is not definitely stated. His mention of the Ungulate resemblances of the molar teeth is significant, seeing that this is a feature which has been often noticed as characteristic of those of *Ælurus*. It may be added that the resemblance of the lower jaw of *Æluropus* to that of *Ælurus* is specially noticed by Professor Milne-Edwards.

Writing at a later date, the late Sir W. H. Flower<sup>1</sup>, who regarded *Ælurus* as the representative of a family connecting the Procyonidae with the Ursidae, assigned *Æluropus* to the last-named family, from the other members of which it differs by the absence of an alisphenoid canal<sup>2</sup>. The genus is described as "an interesting annectant

<sup>1</sup> Recherches Hist. Nat. Mamm. p. 335 (1868-75).

<sup>2</sup> Article "Mammalia," *Encyclopædia Britannica*, 9th ed. vol. xv. p. 441 (1883).

<sup>3</sup> On the page cited above, in the 8th line from the bottom of the first column, the word "An" should be substituted for "No."

viz. Ursidæ, Procyonidæ, and Mustelidæ, placed *Æluropus* in the Ursidæ and *Ælurus* in the Procyonidæ.

My observations on the cast of the skull which was in my charge at Oxford led me to the conclusion that too much weight had been assigned by Flower and Lydekker to the presence in *Æluropus* of the third lower molar, which is lost in *Ælurus* and *Procyon* whilst retained in the Bears. The form of the teeth, especially of the upper fourth premolar (so-called "carnassial") and of the true molars, resembled that of the same teeth in *Ælurus* and *Procyon* rather than that of the same teeth in *Ursus*. The teeth in question are unlike those of any other living Carnivore, recalling those of some of the extinct Ungulata in breadth, squareness, and tuberculation. The general form of my cast of the skull of *Æluropus* differed greatly from that of any Bear. In all Bears the skull is much longer and narrower both in its facial and cranial regions than is the skull of *Æluropus*. Similarly the lower jaw differed greatly in shape from that of the Bears. On the other hand, the relative shortness and breadth of the skull of *Æluropus* are closely repeated in *Ælurus*; whilst the shape of the lower jaw in the two forms I found to be singularly coincident, not only as to outline and curvature of the jaw and coronoid process, but especially in regard to the form of the condyles.

When I entered upon my duties at the Natural History Museum in London, in 1898, I looked up the material relating to *Æluropus* in the Collection, and was much pleased to find that, in addition to a fine skull and mounted skin, the Museum possessed certain of the limb-bones and incomplete feet of *Æluropus*, obtained in 1896.

On comparing these bones—viz., Humerus, Radius and Ulna, Carpus and Metacarpus, Femur, Tibia, Fibula, Tarsus and Metatarsus—with those of *Ursus*, *Ælurus*, and *Procyon*, I found that my previous impression was abundantly confirmed, and that in very important and distinctive points *Æluropus* agrees with *Ælurus* and *Procyon* (more closely with the former) and differs widely from *Ursus*.

I found a strongly marked *entepicondylar ridge and foramen* in the humerus of *Æluropus* (Pl. 20. figs. 1, 1 a). This does not exist in the Ursidæ, but occurs in *Ælurus* and *Procyon* (Pl. 20. figs. 2, 2 a, 3).

Even more remarkable than this were the enormous accessory or extra-carpal bones of the carpus. The ulnar or postaxial extra-carpal (the pisiform of man) is of very large size—larger than in any Aretoid—and springs obliquely backwards and outwards (Pl. 20. fig. 8, *pi.*). But the really extraordinary bone is the preaxial extra-carpal or "præpollex" of some writers, which is articulated to the scapho-lunar and to the preaxial metacarpal, and has the size and position of a sixth metacarpal bone (Pl. 20. fig. 8, *r.e.*).

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form, connecting the true Bears with *Ælurus* and with several extinct genera. Dentition i.  $\frac{3}{3}$ , c.  $\frac{1}{1}$ , p.  $\frac{3}{3}$ , m.  $\frac{3}{3}$ ; total 40. Premolars increasing in size from first to last, and two-rooted except the first. First upper molar with quadrate crown, broader than long. Second larger than the first. Cranium with zygomatic arches and sagittal crest immensely developed, and ascending ramus of mandible very high, giving greater spaces for attachments of temporal muscle than in any other existing member of the order. Bony palate not extending behind the last molar tooth . . . . . Feet bear-like, but soles more hairy, and perhaps less completely plantigrade. Fur long and thick. Tail very short. One extremely rare species, *Æ. melanoleucus*, . . . . . It is of the size of a small brown bear, of a white colour, with ears, spots round the eyes, and limbs black."

This bone has no parallel for size and shape in the Carnivora. A radial extra-carpal of large size has been described in some Rodentia and Insectivora, but in the Carnivora as hitherto described it is always small, and especially small in the larger forms (see Bardeleben, Proc. Zool. Soc. 1889, p. 259).

When we compare the carpus of *Æluropus* with that of the Bears, we find that there is only a very minute bone in *Ursus* corresponding to the large radial extra-carpal of *Æluropus*. In *Ælurus*, on the other hand, a radial extra-carpal of relatively large size—but not so large proportionately as that of *Æluropus*—is present. In *Procyon* the radial extra-carpal appears not to be developed or to be minute.

In regard to this bone, then, *Æluropus* differs markedly from *Ursus* and agrees, though not closely, with *Ælurus*. We are not acquainted with the mechanical requirements in the use and movements of the fore-foot which its presence subserves.

A close comparison of the bones of the forearm of *Æluropus* with the corresponding bones of *Ursus*, *Ælurus*, and *Procyon*, as also of the bones of the thigh and leg of the same genera, confirms in many minute particulars the proposition that *Æluropus* differs from *Ursus*, and agrees with *Ælurus* and *Procyon*, and, moreover, agrees more closely with the former than with the latter of these two (see Pl. 20. figs. 5, 6, 7).

The comparison of the femora is very convincing in this respect, details of the form and curvature of articular faces and of the development of the trochanters showing an amount of minute coincidence as between *Æluropus* and *Ælurus* which can only be interpreted as the indication of close genetic affinity.

Having satisfied myself on these points, I requested Mr. Lydekker, who had not previously examined the limb-bones of *Æluropus*, to go over the specimens and to give me the result of his observations. He entirely accepted my conclusion that *Æluropus* must be removed from association with the Bears, and associated with *Ælurus* and *Procyon*. It has accordingly been removed to that position in the exhibition gallery of the Museum, and is no longer to be spoken of as "the Parti-coloured Bear," but as "the Great Panda."

It seems to me that *Æluropus* is probably an earlier form than either *Ælurus* or *Procyon*, and it would not be surprising were affinities between it and extinct forms discovered. In the meanwhile, the division of the Arctoidea into three families, the Ursidæ, Procyonidæ, and Mustelidæ, may be maintained, with the assignment of *Æluropus* to the Procyonidæ alongside of *Ælurus* and *Procyon*.

One peculiarity of the bones of *Æluropus* should, I think, be placed on record. I refer to their great specific gravity. Not only are the bones (such as the lower jaw and skull-bones) powerfully built and of great actual thickness, but their weight is extraordinary. I do not know any bones of terrestrial Mammalia of similarly high specific gravity.

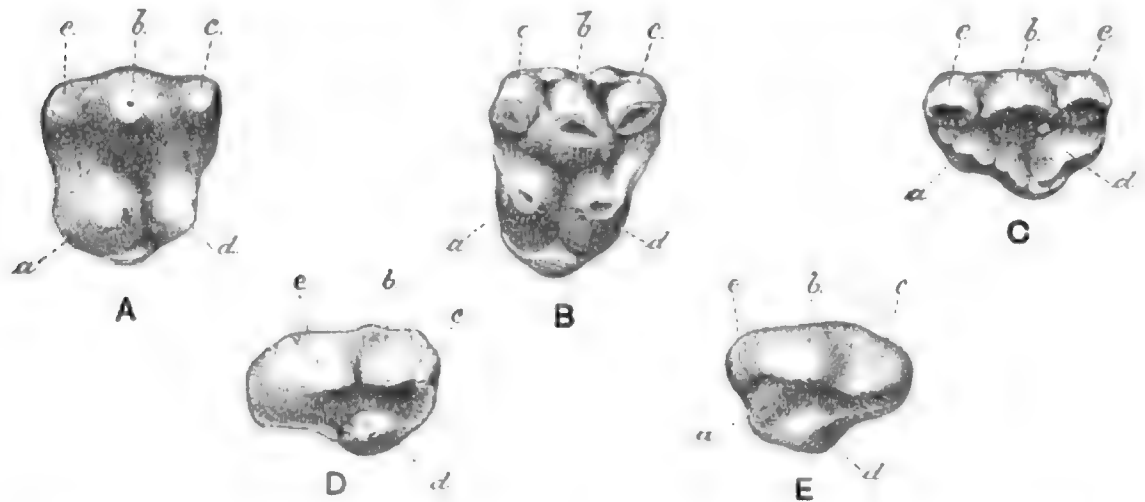
Mr. Lydekker has kindly drawn up for me a minute descriptive account of the skull and limb-bones of *Æluropus* and the details of their comparison with those of *Ursus*, *Ælurus*, and *Procyon*. This account follows.

The illustrations of the skulls and limb-bones given in the Plates have been prepared under my supervision by Mr. Gronwald at the Natural History Museum.

*Detailed Description of the Skull and Limb-bones.*

By R. LYDEKKER, F.R.S.

From *Ælurus* (in which the formula of the cheek-teeth is  $p. \frac{3}{4}, m. \frac{3}{4}$ , and the total number of the dentition 38) *Æluropus* differs markedly, not only by the absence of an alisphenoid canal, but likewise by the presence of a third lower true molar; in the latter respect resembling the Ursidæ, and more especially the extinct genus *Hyænarctus*, in which the upper molars have short and broad crowns, and the last lower molar is much less elongated than in the genus *Ursus*, being, indeed, considerably shorter than the tooth in front of it. The carnassials of *Hyænarctus* likewise come much closer to those of *Æluropus* than to the corresponding teeth of *Ursus*; the upper one of the former genus having a trilobed blade, owing to the development of a style in front of the protocone. Its tubercular portion also carries a small hypocone, which, however, is coalesced with



Left upper carnassial teeth of Raccoon (A), Himalayan Long-tailed Panda (B), Great Panda (C), Cave-Bear (D), and *Hyænarctus* (E). a, protocone; b, paracone; c, metacone; d, hypocone; e, anterior style.

the protocone (fig. E). In *Æluropus*, on the other hand, the upper carnassial (which, contrary to the statement of Sir William Flower, has an inner root) has a large and distinct hypocone situated behind the protocone, from which it is completely separate; this being a character it possesses in common with *Ælurus* and the American *Procyonidæ*, but found in no other Carnivora. In the Raccoon and its American relatives the anterior style of this tooth is, however, much reduced, and as the metacone is also relatively small, the blade, although still trilobed, is mainly formed by the paracone.

The lower carnassials of *Æluropus* and *Ælurus* are likewise constructed on the same general plan, being remarkable for the large size of the metaconid and entoconid. In this feature they are essentially raccoon-like\*, the main difference being that the entoconid is double—distinctly so in *Ælurus*, but rather less clearly in *Æluropus*. In all

\* These features are well shown in the series of sectorial teeth of Carnivora exhibited on one of the pillars of the Lower Mammal Gallery of the Natural History Museum, from which figs. A to E were taken.

three forms the metaconid is placed immediately on the inner side of the protoconid, instead of partly behind it.

We have, therefore, the important fact that *Ælurus* and *Æluropus* resemble the American Procyonidæ, and thereby differ from all other Carnivora, in the presence of two lobes, or cusps, on the inner or tubercular portion of the upper carnassial. And since *Ælurus* has been referred by Mr. Blanford to the Procyonidæ, there is a *primâ facie* presumption that *Æluropus*, in spite of its retention of the third lower molar, is likewise a member of the same family.

Turning for confirmatory evidence first to the external features of the animal, it may be noticed that the type of coloration is essentially unlike that obtaining in the Ursidæ, although a superficial approximation is presented by some specimens of *Ursus pruinosus*. On the other hand, if the coloration of *Æluropus* be compared with that of *Ælurus*, there are certain similarities in the general plan. In both, for example, the limbs are black; and the black ring round the eye of the former corresponds to the chestnut streak running through the same organ in the latter. The fur, too, of both animals is likewise very similar in character, being comparatively sleek and smooth, and unlike the shaggy coat of so many of the Bear tribe. Of more importance is the form and expression of the face, which in both animals is short, broad, and cat-like, entirely lacking the prolonged snout characteristic of the Bears. The ears, too, are strikingly alike in both genera; and the tail, although still very short, is longer in *Æluropus* than in any Bear. The points in which the feet of the former differ from those of the latter are referred to in the above extract from Sir William Flower's description of the genus.

As regards the features in which the skull of *Æluropus* resembles that of *Ælurus* and differs from those of the Bears, mention had been made by Professor Milne-Edwards, and before him by Professor P. Gervais, of some of the most important of these.

Both agree in their relative shortness, wide zygomatic arches, convex profile, and curvature of the inferior margin of the lower jaw, as well as in the great elevation, forward inclination, and hook-like shape of the coronoid process of the latter. The enormous development of the sagittal crest in *Æluropus* causes the convexity of the profile to be more marked than in *Ælurus*. The *Æluropus* skull differs from that of *Ælurus* in the absence of postorbital processes to the frontals, and likewise by the non-prolongation of the palate behind the last molar. In the presence of such processes and the prolongation of the palate, *Ælurus* is the more bear-like of the two, although it has no post-orbital process on the zygoma. On the other hand, *Æluropus* approximates to the Raccoon in the absence of postorbital processes on the frontals, although the Raccoon retains the one on the zygoma. Although by no means so short and wide, the skull of the Raccoon, especially in its profile, is more like those of *Ælurus* and *Æluropus* than is a Bear's skull. A point of resemblance between *Æluropus* and *Ursus* is to be found in the circumstance that the maxillary foramen opens on the side of the skull well in advance of the zygomatic root, whereas in *Ælurus* and *Procyon* it perforates the zygoma itself. As Professor Milne-Edwards has pointed out that in *Æluropus* a depression in the bone indicates the position of the alisphenoid canal, the absence of the canal itself cannot be a feature of any great morphological importance.



In addition to the great peculiarity of their general form, to which allusion has been already made, the jaws of both *Elurus* and *Eluopus* differ from the Ursine mandible by the very remarkable conformation of the condyle.

In the condyle of *Ursus* the articular surface forms a regular semicylinder, with its inner margin approximately at right angles to the long axis. On the other hand, in the two genera under special consideration the articular surface is like a ribband wound obliquely on a cylinder of which the ends have been cut off along the margins of the ribband. Consequently the inner margin of the articular surface forms an angle of about  $45^\circ$  with the axis of the condyle. No marked approximation to this very peculiar type of condyle is exhibited by the Raccoon. In *Elurus* the mandibular "angle" is fairly well developed and nearly continuous with the long axis of the jaw, but in *Eluopus* it is very small and inflected.

As regards the appendicular skeleton, concerning which no description has hitherto been published, the scapula in the Museum specimen of *Eluopus* being wanting, comparison may be commenced with the humerus, which has the proximal epiphysis still separate from the shaft, thus indicating that the animal was not fully adult at the time of its death. Compared with the corresponding bone of *Ursus* (Pl. 20. fig. 4), as well as with that of the extinct *Hyænarctus*, the humerus of *Eluopus* (Pl. 20. fig. 1) is broadly distinguished by the presence of an entepicondylar foramen, in which respect it resembles *Elurus* and the American *Procyonidæ*. But this is by no means the only point of difference from the one type and approximation to the other. To begin with, the head of the humerus in *Eluopus*, *Elurus*, and *Procyon* is much larger in proportion to the rest of the bone than is the case in *Ursus*. Moreover, in the two genera just named the inner margin of the deltoid crest forms a nearly straight line, and the profile of the front surface of the bone makes a slight but regular curve.

In *Ursus*, on the other hand, the inner margin of the deltoid crest is sinuous, and the profile of the bone at the inferior termination of that crest (which forms a marked rugosity) is angulated. In these respects the *Procyon* humerus is nearer to the *Elurus* than to the *Ursus* type. Inferiorly the humeri of *Eluopus*, *Elurus*, and *Procyon* have a marked general resemblance, especially shown by the flatness and expansion, the shallowness and width of the glenoid fossa, and the large size and thinness of the entepicondyle, which is most expanded in *Eluopus*. In *Ursus* the whole extremity is much less expanded, the entepicondyle much more thickened from back to front, and the glenoid fossa much deeper.

As regards the second segment of the arm, the most striking feature in both *Eluopus* and *Elurus* is its extreme relative shortness, the ulna being considerably inferior in length to the humerus, whereas in both the other two genera it is longer. As regards form, the most noticeable feature in the ulna of *Eluopus* and *Elurus* is the much greater elevation of the olecranon above the summit of the greater sigmoid notch when compared with the corresponding bone of *Ursus*. Although the elevation in *Procyon* is less than in the two first-named genera, it is greater than in the third. The radius is, however, perhaps a more important bone in respect to the differences separating *Ursus* from the two genera specially under consideration. In the former (Pl. 20. fig. 7), in

addition to its superior relative length, this bone is specially distinguished by the comparative narrowness of the distal extremity and the sharp point formed by the preaxial malleolus. In *Æluropus*, on the other hand, the distal extremity of the radius (Pl. 20. fig. 8) is much more expanded above the articular surface, and the preaxial malleolus does not descend to nearly the same degree. Consequently the profile of this extremity is quite different from that of the corresponding bone in *Ursus*; while (as may be seen from the figures) there are equally important differences in the contour of the distal articular surfaces of the two bones. In all the above respects the radius of *Ælurus* (Pl. 20. fig. 6) is essentially similar to that of *Æluropus*. Although differing to a considerable degree, the radius of *Procyon* comes nearer to the type of the two latter genera.

Passing on to the manus (Pl. 20. fig. 8), the most noticeable feature in *Æluropus* is the development of a very large preaxial extra-carpal (*r.s.*) in addition to the ordinary ulnar sesamoid, or pisiform (*pi.*). The former is wedged in between the scaphoid process of the scapho-lunar and the first metacarpal, so as to articulate largely with both bones. A precisely similar arrangement obtains in *Ælurus*, although the radial extra-carpal is of very considerably smaller dimensions in that genus. On the other hand, in the carpus of *Ursus* the radial extra-carpal\* is reduced to a small nodule of bone articulating exclusively with the scapho-lunar. In the Raccoons, if such a preaxial bone is developed at all, it must likewise be very minute. The huge size of this bone in *Æluropus*, which simulates a sixth metacarpal, is unique.

Both in *Æluropus* and *Ælurus* the metacarpals are relatively short, this abbreviation being carried to the greatest extent in the former. In regard to this feature *Procyon* departs further from the type of the two genera under consideration than does *Ursus*. Finally, it may be mentioned that the terminal phalanges of *Æluropus* (Pl. 20. fig. 12) and *Ælurus* differ from one another only in point of size, but are quite unlike the corresponding bones of both *Procyon* and *Ursus*. Their most striking common features are their shortness, width, and thinness, coupled with the great relative development of the basal protecting sheath.

The femur of *Æluropus* (Pl. 20. fig. 9) is characterized by its shortness and flatness, as well as by the small antero-posterior extent and nearly symmetrical form of the trochlear surface for the patella. On the posterior aspect (fig. 9*a*) the digital fossa is very deep, and the area between the head and the two trochanters remarkable for its width and flatness. Owing to this, the two trochanters are widely separated from one another. Another feature is the relatively small size of the lesser trochanter, which is situated on the pre-axial border of the shaft, so as to be largely visible in a front view. Although its shaft is proportionally longer and more slender, the femur of *Ælurus* presents the essential features of the corresponding bone of *Æluropus*; and in the femur of *Procyon*, owing to relatively greater shortness and width, the resemblances to the latter are even more strongly marked, although less is seen of the lesser trochanter in a front view. On the other hand, the Ursine femur (Pl. 20. fig. 10) is totally unlike that of the genus under consideration. Not only is the shaft much longer and more nearly cylindrical, but the trochlear surface for the patella is more elongated, and has one lateral border considerably

\* See Flower, 'Osteology of the Mammalia,' p. 287, fig. 93 (1853).

longer than the other. Much more striking are the differences at the proximal end of the hinder surface. Here the area between the head and the two trochanters is narrow and uneven; the trochanters themselves are closely approximated and connected with one another by an oblique ridge; while the lesser trochanter is relatively larger and situated on the posterior surface of the shaft considerably behind its preaxial border, so as to be almost entirely concealed when the bone is viewed from in front.

In a distal view of the femora of *Eluopus*, *Elurus*, and *Procyon* the two condyles have their posterior borders nearly in the same vertical plane, whereas in *Ursus* the inner condyle projects nearly half an inch behind the plane of the posterior border of the outer one.

The evidence of this bone is therefore very strongly in favour of an intimate connection between the three genera first named and their wide differences from the fourth.

The tibia and fibula of *Elurus* correspond with the femur in relative shortness and stoutness. In the tibia the ligament by which the patella is attached springs from a separate ossification of the proximal epiphysis, as is the case in Bears and many other mammals. Perhaps, in addition to its general proportions, the most distinctive feature of this bone is the extreme shallowness of the groove on its distal surface for articulation with the astragalus. In this respect it closely accords with the larger and more slender tibia of *Elurus*, but differs widely from *Ursus*. In *Procyon* the tibia is to some extent intermediate between these two types. As regards the fibula, it will suffice to say that in both *Eluopus* and *Elurus* it is characterized by the great expansion of its two extremities.

In correlation with the shallow grooves on the distal extremity of the tibia, the astragalus of *Eluopus* is characterized by the slight elevation of the ridges on its tibial surface, while above that surface it lacks the projection which is so conspicuous in the corresponding bone of the Bear. Another characteristic feature of the tarsus of the genus under consideration is the antero-posterior elongation of the cuboid—a feature also shared by the tarsus of *Elurus*, but not by that of *Ursus*, in which the cuboid is transversely elongated. To the inner side of the navicular is articulated in both *Eluopus* and *Elurus* a very large tibial sesamoid, which is of a pointed form and extends down by the side of the entocuneiform. I cannot find evidence of the existence of this tibial sesamoid in either *Procyon* or *Ursus*. Both *Elurus* and *Procyon* differ from *Eluopus* in the greater length and slenderness of the metatarsals, this feature, which is doubtless a functional one, being most developed in *Procyon*. It may be added that the cuboid of the latter genus is of the elongated *Eluopus* type.

From the foregoing survey it will be evident that, so far as its dentition and osteology are concerned, *Eluopus* is very closely allied to *Elurus*, the resemblance of some of the bones of the two genera being so close as to suggest specific rather than generic distinction. From *Ursus* the differences presented by the bones of both genera are very marked indeed. As regards the American representatives of the Procyonidae, the dental and osteological resemblances presented by the two genera in question are very noticeable, although in some, but by no means all, respects these are greater in *Elurus* than in *Eluopus*. In its retention of the last lower molar the latter serves, indeed, to connect the former with *Ursus*, *Hyenarctus*, *Amphicyon*, etc.

In spite of this difference in their dental formula, it appears reasonable that if *Ælurus* be included in the Procyonidæ, *Æluropus* should likewise find a place in the same family. The two may indeed be regarded as the representatives of a subfamily group of the Procyonidæ—the *Ælurinae*. And the following characters will serve to differentiate both the family from other Carnivora, and the Old World subfamily from its American representatives :—

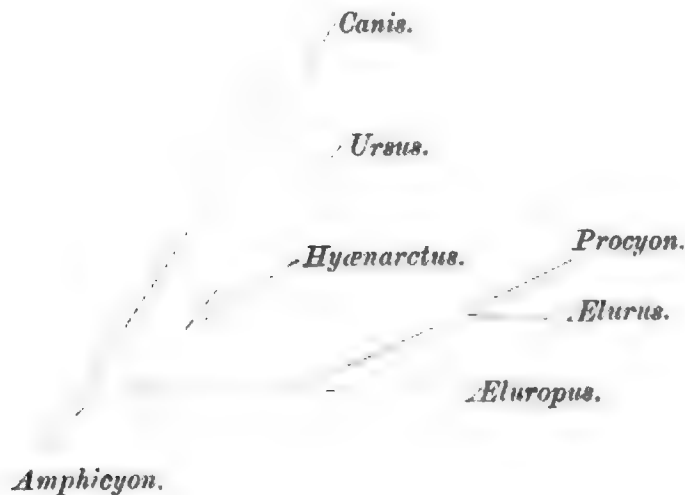
**PROCYONIDÆ.**—True molars  $\frac{3}{2}$ , except in *Æluropus*, where they are  $\frac{3}{1}$ ; tubercular, or inner, portion of upper carnassial formed of two distinct cusps, the protocone and hypocone. Humerus usually with an entepicondylar foramen. Alisphenoid canal wanting, except in *Ælurus*. Feet plantigrade; tail generally long and ringed.

a. *Procyoninae*.—Blade of upper carnassial mostly formed by the paracone. No alisphenoid canal. Two lower molars. Tail long. Steno's fissure present.

b. *Ælurinae*.—Blade of upper carnassial formed to a great extent by the anterior style and metacone, which approximates in size to the paracone, and thus renders the blade completely trilobed. Steno's fissure absent.

1. Tail long; two lower molars, an alisphenoid canal, palate prolonged behind *m. 3*, a postorbital process, radial extra-carpal moderate. . . . . *Ælurus*.
2. Tail rudimentary; three lower molars, no alisphenoid canal, palate not prolonged beyond *m. 3*, no postorbital process, radial extra-carpal very large . . . . . *Æluropus*.

In the retention of the third lower molar *Æluropus* is more generalized than *Ælurus*, but in its rudimentary tail and the obliteration of the alisphenoid canal it displays greater specialization. The retention in both genera of the entepicondylar foramen to the humerus indicates that they must have branched off from the ancestral stock at an earlier date than *Hyaenarctus* and *Ursus*. These relations may be roughly indicated in the accompanying diagram :—



## EXPLANATION OF THE PLATES.

## PLATE 18.

Fig. 1. Palatal aspect of cranium of *Æluropus melanoleucus*; nat. size.

Fig. 2. Left side of palate of *Ælurus fulgens*; nat. size.

Fig. 3. Left side of palate of *Procyon cancrivorus*; nat. size.

Fig. 4. Palate of *Ursus arctus*;  $\frac{1}{2}$  nat. size.

*p.*, carnassial; *pal.*, hinder border of hard palate; *pt.*, pterygoid; *gl.*, glenoid cavity; *t.*, tympanic; *eu.*, eustachian canal; *f.o.*, foramen ovale; *l.p.*, foramen lacerum posterius; *cl.f.*, condylar foramen; *x*, Steno's fissure, the aperture of Steno's duct.

## PLATE 19.

Fig. 1. Upper surface of right half of cranium of *Æluropus melanoleucus*; nat. size.

Fig. 2. Upper surface of right half of cranium of *Ælurus fulgens*; nat. size.

Fig. 3. Upper surface of right half of cranium of *Ursus arctus*; about  $\frac{1}{3}$  nat. size.

Fig. 4. Palatal aspect of right ramus of mandible of *Æluropus melanoleucus*; nat. size.

Fig. 4*a*. Outer aspect of same; about  $\frac{2}{3}$  nat. size.

Figs. 5, 5*a*. Palatal and outer aspects of right ramus of mandible of *Ælurus fulgens*; nat. size.

Fig. 6. Palatal aspect of right ramus of mandible of *Procyon cancrivorus*; nat. size.

Figs. 7, 7*a*. Palatal and outer aspects of right ramus of mandible of *Ursus arctus*;  $\frac{1}{2}$  and  $\frac{1}{3}$  nat. size.

*m.*, carnassial, *na.*, nasal; *p.o.*, postorbital process of frontal; *cr.*, coronoid process of mandible; *b.c.*, base of coronoid process; *c.*, condyle of do.; *d.*, angular process of do.; *i.c.*, internal condylar process.

## PLATE 20.

Figs. 1, 1*a*, 1*b*. Palmar, preaxial, and distal aspects of right humerus of *Æluropus melanoleucus*;  $\frac{2}{3}$  nat. size.

Figs. 2, 2*a*, 2*b*. Corresponding aspects of right humerus of *Ælurus fulgens*; nat. size.

Fig. 3. Distal aspect of right humerus of *Procyon cancrivorus*; nat. size.

Figs. 4, 4*a*, 4*b*. Palmar, preaxial, and distal aspects of right humerus of *Ursus arctus*;  $\frac{2}{3}$  nat. size.

Fig. 5. Dorsal aspect of right radius of *Æluropus melanoleucus*;  $\frac{2}{3}$  nat. size.

Fig. 6. Dorsal aspect of right radius of *Ælurus fulgens*; nat. size.

Fig. 7. Dorsal aspect of right radius of *Ursus arctus*;  $\frac{2}{3}$  nat. size.

Fig. 8. Dorsal aspect of right carpus and metacarpus of *Æluropus melanoleucus*; nat. size.

Figs. 9, 9*a*. Dorsal and ventral aspects of right femur of *Æluropus melanoleucus*; nat. size.

Figs. 10, 10*a*. Corresponding aspects of right femur of *Ursus arctus*; nat. size.

Fig. 11. Dorsal aspect of right tarsus and metatarsus of *Æluropus melanoleucus*; nat. size.

Fig. 12. A terminal phalangeal of *Æluropus melanoleucus*.

*d.*, deltoid ridge; *ent.c.*, entepicondyle; *ent.f.*, entepicondylar foramen; *tr.*, trochlea; *a.*, tuberosity of radius; *pi.*, pisiform; *sc.l.*, scapho-lunar; *tp.*, trapezium; *td.*, trapezoid; *u.*, unciform; *cu.*, euneiform; *r.s.*, preaxial extra-carpal; *h.*, head of femur; *g.t.*, great trochanter; *l.t.*, lesser trochanter; *t.f.*, trochanteric fossa; *cd.*, condyles of femur; *ca.*, calcaneum; *ar.*, astragalus; *t.s.*, tibial sesamoid; *ent.cu.*, entocuneiform; *m.cu.*, mesocuneiform; *ect.cu.*, ectocuneiform; *cb.*, cuboid; *na.*, navicular.









VII. *On the Intestinal Tract of Birds; with Remarks on the Valuation and Nomenclature of Zoological Characters.* By P. CHALMERS MITCHELL, M.A., D.Sc. Oxon., F.L.S., F.Z.S., Lecturer on Biology at the London Hospital Medical College.

(Plates 21–23.)

Read 21st March, 1901.

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### INTRODUCTION.

IN 1813, in one of a series of papers on the Solvent Glands and Gizzards of Birds, Sir E. Home (15) gave a description and some measurements of the intestines in the Ostrich, Emu, Cassowary, and Rhea; and in 1814 (16) the same author described the course of the intestines and the form of the caeca in a number of birds, giving figures, in which, however, the coils were represented as freed from their blood-vessels and mesenteries. In the second edition of the 'Leçons' Cuvier (5) described the arrangement of the intestinal tract in some dozen birds and distinguished regions, as the "duodenal loop";

the "median loop," extending from the duodenum to the unpaired cæcum; the "colic loop," extending from the median loop to the insertion of the paired cæca; and the "rectum." Following Meckel, he identified the "unpaired cæcum" as the rudiment of the yolk-sac. Cuvier, however, had no great range of facts before him, and refrained from any general conclusions. Owen, in Todd's 'Cyclopædia of Anatomy and Physiology' (31), added little to the investigations of Home and Cuvier; and Macgillivray (22) did little more than to point out that the subject might yet afford useful facts for taxonomy. Thereafter the subject was apparently completely neglected until Dr. Gadow (10, 11, 12) began his extensive and extremely interesting investigations. Gadow studied and figured the loops and blood-vessels in a large number of forms, distinguished the loops of the intestine as being "open" or "closed" according to the width of the mesentery between the limbs of the fold, named the folds "right-handed" or "left-handed" according to the position of the descending limb; but, above all, described at length and based taxonomic distinctions on the mode in which the loops were folded within the cœlom.

In 1894, working in the Prosectorium of the Zoological Society, I examined the intestines of a number of birds in the method from which Gadow obtained his notable conclusions; but I found not infrequently that there were individual variations in the disposition of the loops, particularly as regarded their "right"- and "left-handedness," no doubt in connection with the writhing movements of the gut during life, and came to the conclusion that there was more to be learned from investigation of the relation of the loops to the unfolded mesentery than from consideration of the mode in which the folds were packed. The method of examination, which I have since found to be an extension of Cuvier's method, I described in 1895 (25), and, at greater length, in 1896 (26). It depends on the morphological nature of the intestinal tract of Vertebrates, which is a tube suspended in the cœlom by a fold of mesentery attached to the dorsal wall. The tube, in its course, describes an arc between two fixed points, the pyloric end of the stomach anteriorly, and the insertion of the rectum to the cloaca posteriorly. A third fixed point is given in the embryonic stage by the attachment of the yolk-sac nearly in the middle of the ventral edge of the arc, and this point is often marked in the adult by Meckel's diverticulum (see *infra*, p. 175). The intestinal tract increases considerably in length between the fixed points, and along with its mesentery, which similarly increases, it is thrown into a series of loops which are folded on one another in the various modes described by Gadow. When the intestines have been removed from the bird by section at the pylorus and cloaca and by cutting the mesentery along its dorsal attachment, the cut end of the duodenum and of the rectum may be pinned on a board to the operator's right-hand, these two points and the cut edge of the mesentery stretching between them being placed in their natural relative positions. Then, with some trouble in the more complicated cases, the various loops may be unfolded to the left and pinned out; whereupon the mesentery appears as a flat sheet, in shape roughly the segment of a circle, the cut dorsal edge of the mesentery being the sector, and the arc, which carries the intestinal tract, being irregularly distorted. The sheet of mesentery is of course double, and the blood-vessels and autonomic nervous system run between the two sheets, being situated outside the cœlom. The figures which illustrate

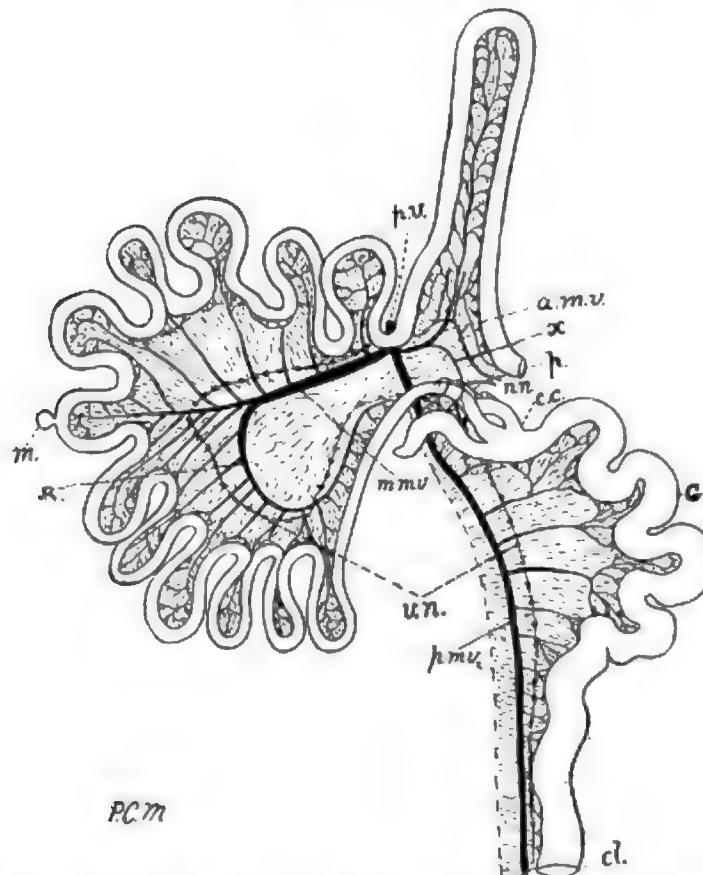
this memoir represent the intestinal tracts of various birds as seen in preparations of the kind described, and therefore illustrate the morphological conditions of the tracts. In 1896 (26) I had already a considerable material, and described and figured some of the chief modifications of the common type displayed in the groups of birds. Since then I have been able to add largely to my material. I have now examined many hundreds of birds, including a number of rare forms, and representing nearly all the important groups of birds. Taking the System given by Dr. Gadow in Bronn's 'Thier-Reich,' vol. vi. part ii. pp. 299-301, as one specially familiar to anatomists, I find that my material includes, so far of course as living forms go, all the groups of Ratites, and, of Carinates, all the Orders, all the Suborders except *Mesites*, and all the Families except *Mesitidæ*, *Galbulidæ*, and some Passerine families. For materials I am indebted to the authorities of the National Collection, who have allowed me to examine a number of spirit-specimens, to several private persons, including in particular Mr. C. Hose of Borneo through Mr. Beddard, but above all to the Zoological Society of London. Nearly all the work was done at the Prosectorium on materials from the Gardens or sent to the Prosector. To my friend the Prosector, Mr. Beddard, F.R.S., I am deeply indebted both for materials and assistance. To Prof. Howes, F.R.S., I am indebted for many valuable references to literature, and I have had the advantage of discussing the nomenclature of characters with Prof. Ray Lankester, F.R.S.

#### THE TRACT IN *PALAMEDEA CORNUTA* AS AN ARCHECENTRIC TYPE.

It is convenient to describe the conditions of the intestinal tract in one form in some detail so as to provide a standard for comparison and to avoid unnecessary repetition. In a former paper (26. p. 138, fig. 2) I took the condition in an embryo of an Argus Pheasant, about thirty days old, as a starting-point; here, for various reasons which will appear later, I begin with the condition in the Horned Screamer, *Palamedea cornuta* (fig. 1). When unfolded, in the fashion already described, the intestinal tract is seen to present three main portions between the pyloric cut end (*p.*) and the cloacal cut extremity (*cl.*). The first division from *p.* to the point where, at *p.v.*, the cut portal vein is represented consists of a long, narrow, and closed loop; this is the duodenal loop of Cuvier: it contains the pancreas between its ascending and descending limbs, and receives the ducts of the pancreas and liver. It always in the undisturbed condition lies bent backwards towards the cloaca, ventrad of all the other loops, and is therefore the first portion of the gut to be seen when the abdomen is opened from the ventral surface in the usual fashion. Its ascending and descending limbs are held together by a narrow outgrowth of the mesentery. The mesentery, after leaving the duodenum, expands into a large, nearly circular fold, at the circumference of which, from the end of the duodenum to *c.c.*, the point of insertion of the cæca, is suspended the great portion of the intestine. About the middle of this portion is situated Meckel's Diverticulum (*m.*), which is well known to be a relic of the embryonic stalk of the yolk-sac (*cf.* 26. fig. 2). This portion I name Meckel's Tract, as it carries Meckel's diverticulum. In *Palamedea* it presents a number of minor, simple corrugations, but in more specialized forms the loops present extremely definite and well-marked types of divergence from

this simple condition. Cuvier (5) divides this median portion into an "*Anse moyenne*," extending from the duodenum to Meckel's diverticulum, and an "*Anse colique*," from the diverticulum to the insertion of the cæca. The examination of a larger number of types, however, shows that although the remains of the yolk-sac when present give a point of orientation, still there is not a natural point of division between the loops at the insertion of the yolk rudiment, which, indeed, most frequently lies at the summit of a minor loop. Moreover, the adjective "colic" rightly belongs to a lower

Fig. 1.



Intestinal Tract of *Palamedea cornuta*. From *p.* to *p.v.* is the Duodenum; from *p.v.* to *c.c.*, the insertion of the cæca, is Meckel's Tract; from *c.c.* to *cl.* is the Large Intestine, here convoluted in its anterior portion, *G*\*.

*p.v.*, portal vein; *a.m.v.*, anterior mesenteric or duodenal vein; *m.m.v.*, middle mesenteric vein; *p.m.v.*, posterior mesenteric or rectal vein; *x*, "bridging" factor of duodenal vein from cæca; *R*, recurrent factor of middle mesenteric vein; *p.*, pylorus; *m.*, Meckel's diverticulum; *cl.*, cloaca; *nn.*, nerves entering mesentery; *v.n.*, "visceral nerve," ganglionated chain of the autonomic nervous system.

portion of the gut, as the colon of mammalian anatomy, from which the name was taken, is not the portion on which Meckel's diverticulum may be found. It is worth noting, however, that very often a change in the colour of the gut, denoting a phase in the digestive processes, begins just distal to the diverticulum. Meckel's tract, in the

\* Since the large intestine is, with few exceptions, short in birds and but rarely differentiated into anything comparable to a colon, it will be simpler to refer to it in this Memoir as *rectum*.



undisturbed condition, lies very irregularly folded, or rather crumpled-up dorsad of the duodenum and ventrad of the rectum. Its posterior portion is nearly straight, an extremely common state. The rectum or third portion of the gut extends from *c.c.*, the end of Meckel's tract, to *cl.*, where it enters the cloaca. It is suspended by a long straight piece of mesentery continuous with the mesentery of Meckel's tract. In the figure, as in some of the later cases, the rectum is represented as folded over to the right so that the cut edge of the mesentery from the duodenum to the cloaca is twisted on itself at the point where the cæca are inserted. The large intestine in most birds is extremely short; its condition in *Palamedea*, where it is convoluted and might be divided into colon and rectum, is unusual. The calibre of the gut varies: the condition seen in *Palamedea* is very usual; the duodenum is wider than Meckel's tract, and the rectum is wider than either that or the duodenum. The cæca are equal in size and of moderate length, being intermediate between the short thick stumps of Passerines and the extremely long, irregularly dilated pouches of the fowl. The blood-vessels, shown in black in this and the subsequent figures, are the veins. At *p.v.* is represented the cut edge of the main portal vein on its way to break up in the liver; the large factor from the stomach and spleen is not represented, but the three characteristic intestinal factors are figured. These are the *anterior mesenteric* or *duodenal*, draining the duodenum, and at *x* receiving a small factor which runs forwards from the cæca and posterior part of Meckel's tract. The draining of these parts of the intestine by a tributary or tributaries of the duodenal vessel is seen here in a simple form, but, as will be seen later, becomes a peculiar and important structural feature. The second or *middle mesenteric factor* of the portal drains Meckel's tract; its main axis runs from Meckel's diverticulum, but a strong factor, which I call the "recurrent mesenteric," curves round from backwards following the contour of the tract. The *posterior mesenteric*, or *rectal* factor, drains the rectum; in many birds it arises from two factors which run backwards along the ventral surface of the kidneys and join opposite the junction of the rectum and cloaca, entering the rectal mesentery at that point. These three components of the portal correspond to the three main divisions of the intestines—the Duodenum, Meckel's tract, and the Rectum; they meet nearly at the same point, but, in different birds, the order of their joining to form the common portal differs; and, after giving considerable attention to the matter, as I cannot find significance in the order of their junction, I shall not refer to it in this memoir. The arteries of the mesentery are small relatively to the veins; their minor branches follow the minor branches of the veins fairly closely; the main branches arise from the dorsal aorta. The dotted chain marked *v.n.* in the figure is the part of the "autonomic nervous system" which follows the intestine. It is extremely plain in some birds, as in *Palamedea*, where it consists of a ganglionated chain following the general contour of the intestinal loops. The nature of my material has not allowed me to follow it out in the majority of my specimens. To certain general points in relation to it I shall recur later.

## VALUATION AND NOMENCLATURE OF CHARACTERS.

In the description of the structure of an organ or anatomical part as it occurs in a large series of different forms, it becomes necessary from simple convenience to attempt some kind of valuation according to which the series of facts shall fall into definitely-named groups. When there is attempted the difficult passage from descriptive anatomy to morphology, it is necessary that the valuation and nomenclature should be in relation to the theory of descent with modification. I assume that birds were monophyletic in origin, and that the existing forms have branched out in diverging directions from the ancestral group. The members of this ancestral group, at the stage when they first might have been called birds, possessed an heritage of characters and tendencies, and these characters and tendencies have undergone modifications different in amount and nature in the different groups. The first business is to come to a decision as precise as possible as to the ground-plan, or archetype, the most ancestral condition of the structures under consideration. In the present case, I find that the condition of the gut in *Palamedea* (fig. 1) may be taken (after allowance for its length, as it is a large bird and vegetarian) as representing closely the ancestral type. The form of the gut is extremely simple; it is distinguished from the intestinal tract of reptiles chiefly by the fact that the three divisions—the duodenum, Meckel's tract, and the rectum—are sharply marked off one from the other. Meckel's diverticulum, the morphological median point of Meckel's tract, occurs nearly at the actual median point. The pair of cæca are of moderate length and are functional. The arrangement of the veins is also extremely simple. It will be seen in the systematic part of this memoir that it is not difficult to refer the more complicated types of arrangement of the tract to the condition in *Palamedea*. I propose to call such a condition "archecentric," implying that it represents a primitive, ancestral, or central condition, from which the conditions to be found in the other cases have diverged. It is obvious that the possession by two or more groups of birds of a character in its archecentric form cannot be an indication in itself that these groups are more closely related to one another than they are to groups possessing the character in another form; for if the diagnosis of archecentricity be correct, the condition has been present in all birds, and may be retained by any. For example, I have recently (28, 29) endeavoured to show that the condition in the wing known as diastataxy is archecentric; that is to say, that in the ancestral wing there was a gap in the series of quills proximad of the fourth secondary quill. If that be correct, the fact that two groups of birds possess diastataxic wings is no reason for uniting the groups.

When the ancestral condition is modified, it may be regarded as having moved outwards along some radius from the archecentric position. Such modified conditions I propose to call "apocentric." Again, it must be obvious that the mere apocentricity of a character can be no guide to the affinities of its possessor. For instance, in the work on the wing of birds, to which I have already referred, I tried to show that the condition of the wing known as eutaxy is apocentric; that is to say, that it is a modification of the archecentric condition, which in this matter is the condition termed diastataxic. Before deciding as to the value of eutaxy in a natural classification, it would be necessary

to decide whether the modification of the archecentric condition were a simple change that we might expect to occur in independent cases, or if it involved intricate and precisely combined anatomical changes that we could not expect to occur twice independently. In fact, having come to the conclusion that a character is apocentric, we must pass on to consideration of the problem whether or no the apocentricity be *uniradial* or *multiradial*. In the case of eutaxy I came to the conclusion that it was the result of a simple closing of the quill series, which might have occurred repeatedly, and probably did occur repeatedly, and that therefore it was an instance of what I call here "multiradial apocentricity." Similar and common multiradial apocentricities, from which no direct argument of kinship is to be drawn, are to be found in conditions depending on the degeneration of a structure. If, for example, the presence of basipterygoid processes be archecentric in birds, their absence is a multiradial apocentricity from which no direct argument as to affinity may be drawn.

These multiradial apocentricities lie at the root of many of the phenomena that have been grouped under the designation "Convergence." Especially in the case of manifest adaptations, organs belonging to creatures very far apart genealogically may be moulded into conditions which are extremely alike. It is of course the business of science to distinguish the dissimilarities of genetic material under the similarities which are the results of adaptation to a common purpose. Ray Lankester (20) long ago designated such parallelism of modifications as Homoplasy; and there seems little reason to doubt that a careful discrimination and elimination of the homoplastic features in so-called cases of convergence would leave a residuum plainly showing the genetic differences, and dispelling many of the hazy ideas which have been grouped round the word convergence. In the case of the alimentary canal, it is easy to set apart certain modifications as directly adaptive, and as therefore of no value when the character of an organ is being considered as an indication of the natural affinities of its possessor. For the apocentric modifications in question have been produced in different mammals as well as in different birds, and hence in birds these modifications must be multiradial and no indication of relationship. I find in the intestinal tract of birds four plain homoplasies—that is to say, four kinds of adaptation which produce multiradial apocentricity; three of these are well known, the fourth, so far as I am aware, has not yet been pointed out. That all four occur among mammals as well as among birds is a fortunate circumstance that definitely proves their multiradial character.

*First Homoplastic Modification.* Lengthening of the gut in graniviferous and grazing birds.—This feature has been well known for long, and is in obvious relation to the circumstance that the nutrient constituents of the food of such creatures are in a form difficult to digest and in intimate admixture with a large bulk of indigestible material. Much time and much surface are required for digestion and absorption, and these are provided for by increase in length of the gut.

*Second Homoplastic Modification.* Lengthening of the gut with thickening of its wall and relative decrease of its calibre in piscivorous birds.—The very long and narrow gut with stout walls is known in birds and mammals. The small calibre and thick wall are doubtless a protection against mechanical injury by sharp bones. The extreme

length is at first surprising, as we are accustomed to regard fish as being readily digestible. However, a bird does not eat fish carefully with a knife and fork, but bolts it whole. Dr. Hutchison, a recent writer on foods (17), calls attention to the large amount of waste matter in uncooked fish, amounting to fully seventy per cent.

*Third Homoplastic Modification.* Shortening of the gut in frugivorous birds.—The tendency of the gut in birds and mammals which live chiefly on fruit to be very short, thin-walled, and wide is well known, and is in direct relation to two simple physiological factors. The nutritious substances in fruits are in a form which renders them capable of rapid and fairly complete absorption, and the organic salts present stimulate osmosis. The ease of absorption makes a relatively large surface unnecessary, and the large calibre of the gut not only diminishes the outflow from the blood caused by the presence of organic salts, but it decreases the danger of violent purging. The vigour of peristalsis in birds is remarkable; when the duodenum of a pigeon contracts it becomes as hard and tense as a piece of cartilage.

*Fourth Homoplastic Modification.* Increase of length rather than of calibre in large birds.—I am not aware that the circumstance has been noticed, but it is the case that in large birds and large mammals the gut tends to be relatively longer than in small birds and small mammals. The explanation, I think, is simple. In the course of phylogenetic increase in size, the various organs increase in size correlatively with the whole, but in a mode corresponding to their functions. The first business of the intestine is to present to the food-absorbing surface sufficient to supply the needs of the whole body. As the calibre of a tube increases, its capacity increases more rapidly than its surface; it follows that to preserve the same relation of intestinal surface to intestinal capacity, the length of the gut must increase more than the calibre in the course of phylogenetic increase of size. It is interesting to notice that the caeca and the rectum, two portions of the gut of birds in which absorption is not so great, increase in large birds almost as much in calibre as in length, so that very frequently large birds display caeca and rectum which appear to be much wider than the anterior portions of the intestinal tract. It is plain, from what has been said, that no genetic significance is to be attached to such conditions, which are merely a result of the homoplastic modification due to large size of the whole creature.

There is no need to discuss here the difficult problems as to the mode of origin of homoplastic resemblances. To some extent they may be freshly epigenetic in each generation; and Gadow's (12) investigations into the lengths of the gut in chicks as compared with adults would seem to show that there is much to be learned as to the occurrence of changes of form and length in direct relation to changes of diet. They may have come about by a slow selection of strains with genetic variations in the direction of increased length or of capacity to acquire increased length at the stimulation of food; or, on neo-Lamarckian principles, they may be the summations of the effect of stimulations in a series of generations. It is enough to state that these homoplastic modifications must be allowed for or "corrected" before the drawing of conclusions as to relationship. Before the condition of an intestinal tract can be taken as affording a clue to the affinities of its possessor, it must, in imagination, be shortened, in the case

of a large bird, or a graminiferous or piscivorous bird, or lengthened in the case of a frugivorous bird. In more general terms: when we are satisfied that an apocentricity is multiradial, as is certainly the case when it is homoplastic, we must neglect it when we are dealing with the one character as a guide to affinity (fig. 2).

Fig. 2.

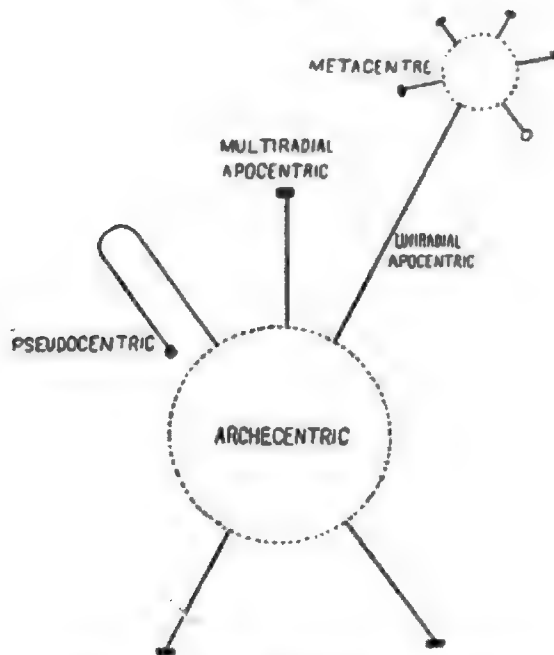


Diagram to explain Nomenclature of Characters.

A complex apocentric modification of a kind that we cannot well expect to be repeated independently, and that may be designated as uniradial, must be the most certain guide to affinity. It happens frequently that such a modification forms a new centre around which new diverging modifications are produced. Such a centre I propose to call a "Metacentre," borrowing a convenient term from physics. It is obvious that the condition of a character, archecentric so far as the whole group of birds is concerned, is metacentric with regard to the common stock of birds and reptiles, and that the transformation of an apocentric character into a metacentre is simply an event in the general process of divergent evolution. I justify the nomenclature which I am proposing largely because it brings the valuation and classification of characters into line with our conception of the general process of evolution.

Finally, there remains to distinguish a form of apocentricity extremely common and often perplexing. Such conditions are marked by an apparent simplicity that, however, reveals its secondary nature by some small and apparently meaningless complexity. Such a condition that mimics the archecentric condition but which can be distinguished from it, I propose to call "Pseudocentric."

I trust that the ideas underlying this attempt at the valuation and nomenclature of characters, so far from being novel, are merely a codification of criteria in common

employment among naturalists. I find, however, that such a codification was necessary when I tried to arrange systematically the modifications of the characters with which this memoir deals. So far as I have used them in my own work, I have found them illuminating, and I offer them in the conviction that the rigorous discipline which their use entails would prove of general utility.

### SYSTEMATIC DESCRIPTION.

The Classification according to which this part is arranged is that given by Gadow in Bronn's 'Thier-Reich' (12).

### RATITÆ.

**CASUARI.**—In the Cassowaries and Emus the gut is archecentric in character. The three regions are well marked; the duodenum is wide in the Cassowary, but longer and narrower in the Emu. In both, Meckel's tract is nearly circular in form, with well-marked minor folds in the Emu, and, in both, with a distinct relic of Meckel's diverticulum about the middle of its course. The rectum is short and nearly straight, this being the only divergence from the archecentric character and a divergence displayed by the vast majority of birds. The loops are drained by the characteristic factors of the common portal vein. The cæca are of moderate length as in the type. I have already given a figure of the gut in the Cassowary (26. fig. 3).

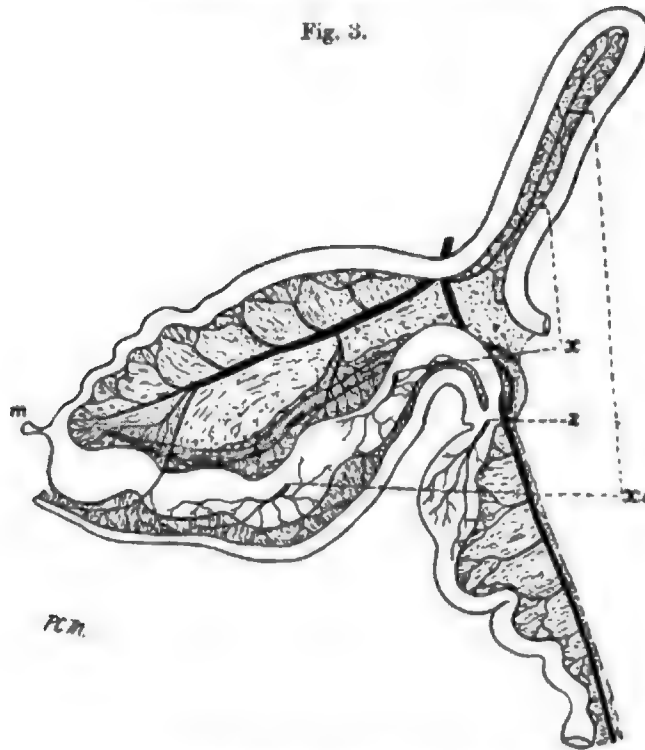
**STRUTHIONES.**—The Ostrich (26. fig. 4) is also markedly archecentric. The divergences from the archecentric type are very slight: the duodenum is rather longer and has a minor loop situated on its distal limb; the rectum is enormously long, being in fact at least equal in length to the first two portions together; the cæca also are extremely long. The factor of the duodenal vein from the cæca comes off rather further from the main stem of the portal vein, and instead of running forwards within the mesentery, it leaves the mesentery and in consequence must be separated when the intestine is unfolded: in this condition it forms what I call a "bridging" vein.

**RHEÆ.**—In *Rhea americana* (fig. 3) the gut is archecentric, and indeed can be distinguished from that of *Palamedea* only in two points. Meckel's tract is somewhat elongated, Meckel's diverticulum lying at its apex, and the cæca are much longer relatively. The region of the cæca is drained by two "bridging" factors of the duodenal vein which leave the mesentery and have to be divided when the duodenum is unfolded outwards. A slight peculiarity that I have noticed in no other bird is that a factor of the splenic vein (fig. 3, z) drains the proximal portion of the rectum.

**APTERYGES.**—The gut of the *Apteryx* (fig. 4), while markedly archecentric, is the most modified of those among Struthious birds. The duodenum and the rectum conform to type, save that the rectum is relatively shorter and is straight. The greater portion of



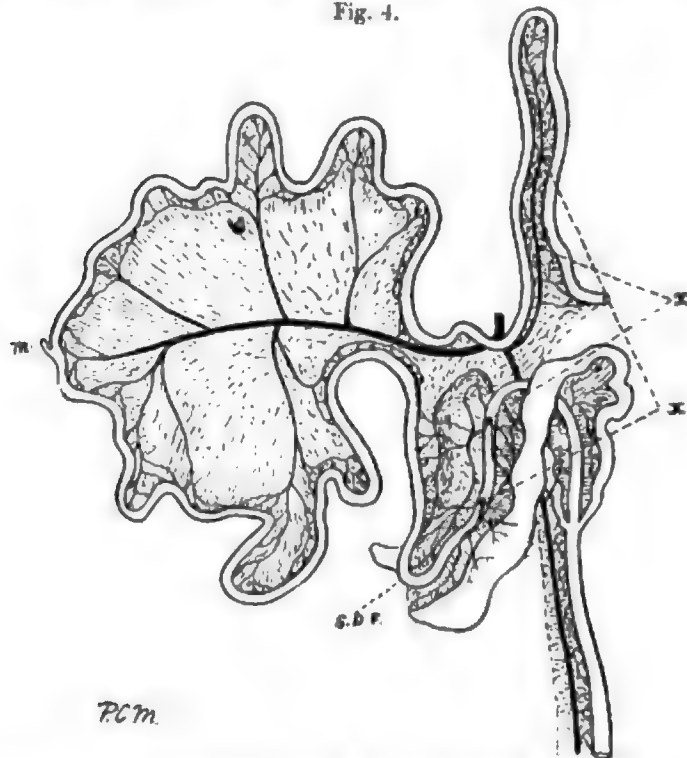
Fig. 3.



Intestinal Tract of *Rhea americana*.

*x, x'*, cut ends of "bridging" factors of duodenal vein, draining the distal portion of Meckel's tract and one caecum; *z*, factor of the splenic vein. General description as in legend of figure 1.

Fig. 4.



Intestinal Tract of *Apteryx Mantelli*.

For explanation, see legends of figs. 1 and 3. *S.D.F.*, apex of supra-duodenal loop.



Meckel's tract forms a large circular fold with Meckel's diverticulum at its central point, opposite the origin of the middle mesenteric vein, as in the archecentric type. But the posterior portion of the tract, that to which the very long caeca are attached, is specialized into a distinct minor loop. This I call the *supra-duodenal loop*, because, in the natural condition of the intestine, it lies directly above the duodenum and is drained by factors of the duodenal vein. This loop in *Apteryx* is the first appearance of a specialized structure to which I shall have to direct repeated attention.

When correction has been made for the obviously homoplastic modifications in the intestinal tract of Ratites—that is to say, when a reduction has been made in the case of the larger forms for size and in the case of the herbivorous forms,—it is plain that while all are archecentric, the Casuarii are by far the least modified, and that in this as in many other characters they deserve the position assigned them as extremely primitive types. *Struthio* and *Rhea* are more modified, and the modification is in the same direction in each. *Apteryx* stands somewhat apart from the others, the specialization of the supra-duodenal loop being well marked in it. The general character in all, however, is so plainly archecentric that no argument can be drawn from the intestinal tract for or against the polyphyletic nature of the group. Such similarities as they present to one another or to other groups are simply part of the common inheritance of all birds.

## CARINATÆ.

### COLYMBIFORMES.

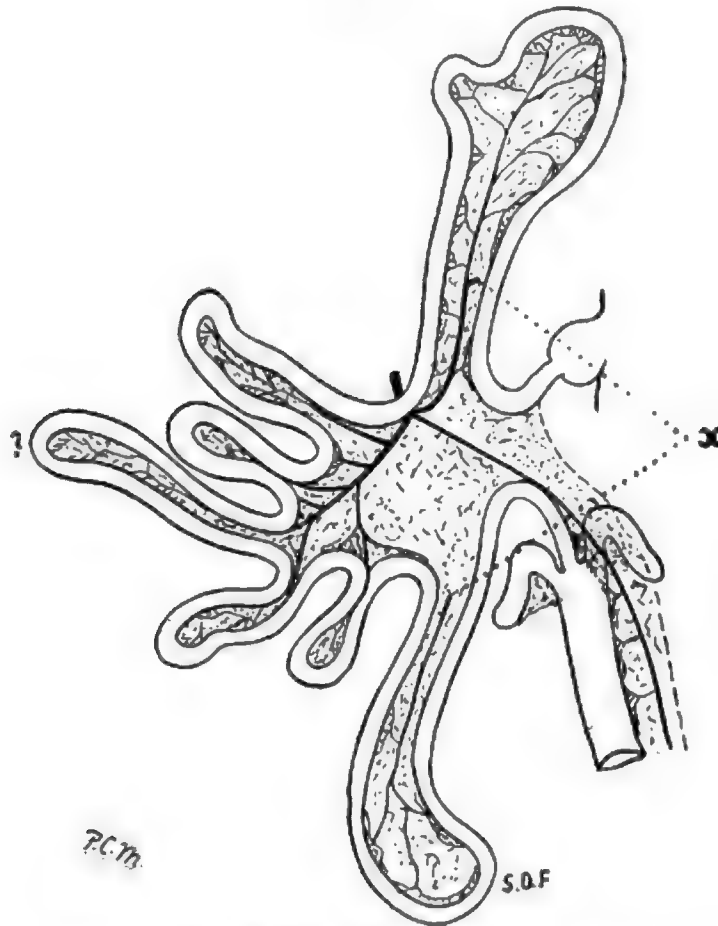
COLYMBI.—I have examined the Great Northern and Red-throated Divers (*Colymbus glacialis* and *C. septentrionalis*), and have already figured the intestinal tract (26. fig. 5). The duodenal loop is straight and normal; the rectum is straight and very short. Meckel's tract is pulled out into a series of short, straight, symmetrically arranged loops with the Meckel's diverticulum nearly at the middle of its course, and with a well specialized supra-duodenal loop drained by a bridging factor of the duodenal vein. The three main factors of the portal vein are typical, and the caeca are of moderate length. It is clear that the Divers present a certain degree of apocentricity in the gut. The fish-eating habits have lengthened the tract, but the increase of length takes place not by a series of irregular loopings but in a definite fashion.

PODICIPEDES.—In the Crested Grebe, *Podiceps cristatus* (fig. 5) the duodenum is a large loop somewhat wider distally. Meckel's tract is still more specialized than that of the Colymbi. It presents first a long minor loop, then a short loop, then a long loop, on which, from the arrangement of the blood-vessels, I suppose the yolk-sac to have lain, although it is not represented by a Meckel's diverticulum; then follow two short loops, and then a very large supra-duodenal loop with characteristic bridging vein. The caeca are relatively short, but wide and functional, and the rectum is short and wide.

In *Tachybaptus fluviatilis*, the Little Grebe (fig. 6), the apocentricity seen in the Crested Grebe is carried further in two points, otherwise the character of the tract is

similar. Two of the minor loops of Meckel's tract are carried out to a great length, one of them bearing Meckel's diverticulum at its summit; the cæca are relatively much longer, and the supra-duodenal loop is still more highly specialized. The Podicipedes, then, present an apocentricity rather more marked than that of the Divers.

Fig. 5.



Intestinal Tract of *Podiceps cristatus*.

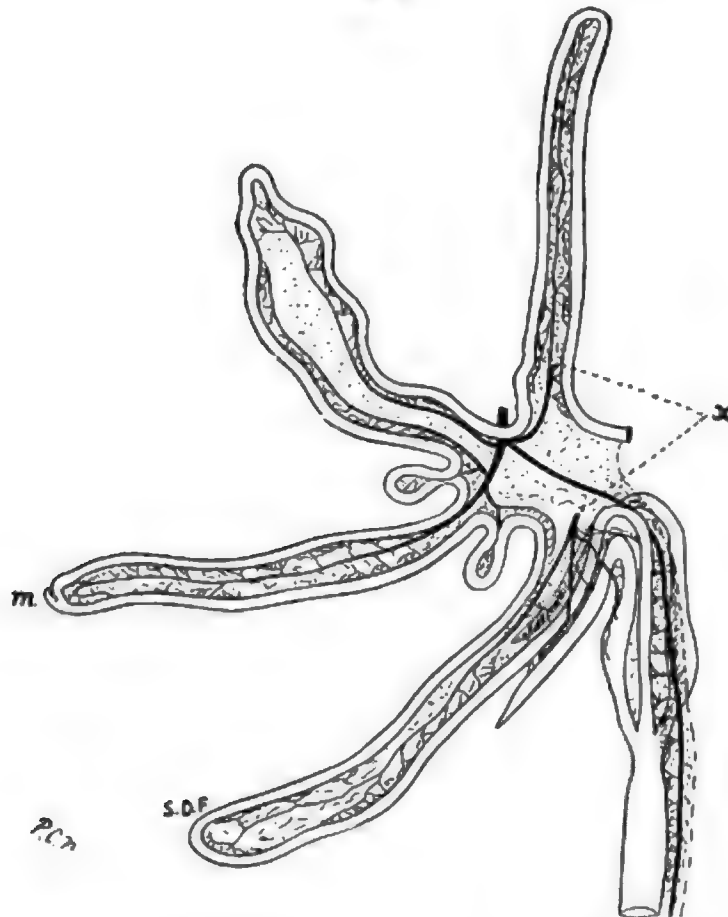
*x*, bridging factor of the duodenal vein draining *S.D.F.*, the supra-duodenal loop; *?*, probable position of Meckel's diverticulum.

When allowance has been made for the size and piscivorous habits of the Colymbiform birds, it appears that while the character of the gut has moved outwards from the arche-centric position chiefly in the direction of the formation of specialized straight loops (according to Gadow's nomenclature, the folding is orthocœlous), the apocentricity is not great, and is certainly not of such a uniradial character as to associate them closely with any other group.

## SPHENISCIFORMES.

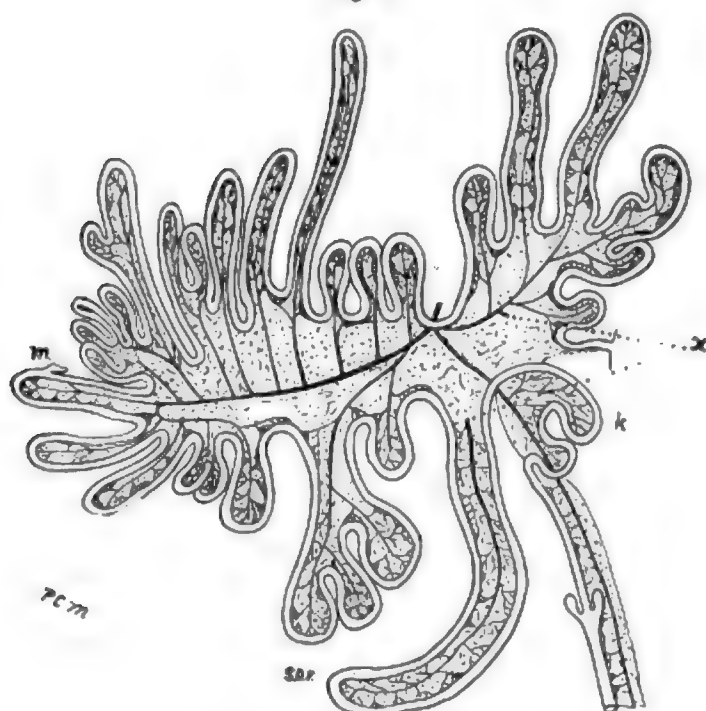
I have already described and figured the intestinal tract of *Eudypetes* (26. fig. 6). I now am able to add descriptions of the condition in *Spheniscus demersus* (fig. 7) and *Aptenodytes Pennanti* (fig. 8). In all three the intestine is extremely long and of

Fig. 6.

Intestinal Tract of *Tachybaptus fluvialis*. Lettering as before.

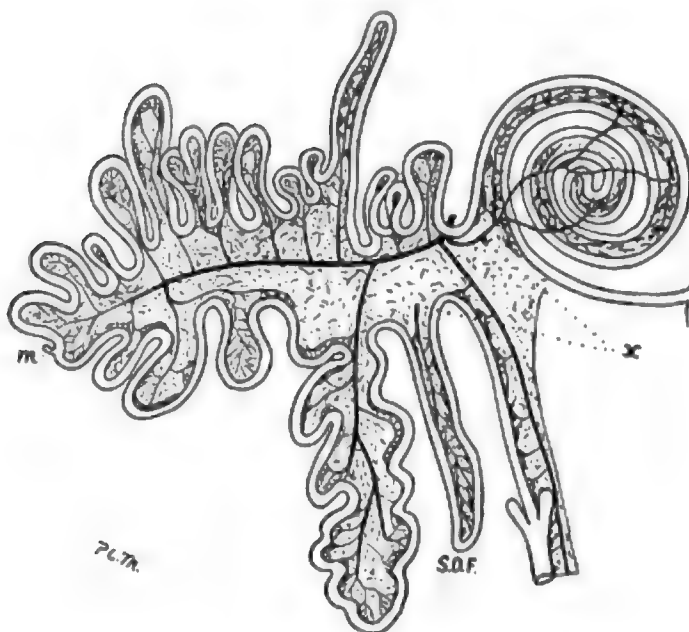
slender calibre with firm walls; in the figures the actual length is somewhat underestimated, so that the "correction" for piscivorous diet has been made partially. The three portions of the tract are well marked and are each drained by a characteristic factor of the portal vein. The duodenum is extremely long; it is thrown into a complicated set of minor loops resembling the condition in the fish-eating Eagles, in *Eudypetes* and *Spheniscus*; in *Aptenodytes* it forms a loosely rolled spiral, a mode of packing increased length that is not at all uncommon among birds and that must be regarded as a multiradial apocentricity. Meckel's tract in all three is moderately specialized; Meckel's diverticulum lies nearly at the middle of its course, but there is a strong tendency for the numerous minor loops to be extended in length or expanded

Fig. 7.



Intestinal Tract of *Spheniscus demersus*.  
k, supra-caecal kink; other lettering as before.

Fig. 8.



Intestinal Tract of *Aptenodytes Pennanti*. Lettering as before.

into minor systems. Of these, two are well-marked in all: a very large loop towards the distal extremity of Meckel's tract and drained by a factor of the middle mesenteric vein, and a long narrow supra-duodenal loop which is drained by a "bridging" factor of the duodenal vein. In *Spheniscus* the portion between the supra-duodenal loop and the rectum, which is very long in all, is expanded into a minor fold, an arrangement characteristic of the Eagles, and to which I give the name "supra-cæcal kink." The rectum in all is extremely short, and the cæca are vestigial in those that I have examined, but Gadow mentions that they were relatively long in a *Eudytes*.

It is plain that the character of the tract in the Sphenisciformes is markedly apocentric. When due allowance has been made for the piscivorous lengthening, the form still remains apocentric: the short cæca, the tendency to form minor loops, the supra-duodenal loop, the tendency to form a supra-cæcal kink, and the extremely short rectum make up a peculiar and distinct type.

#### PROCELLARIIFORMES.

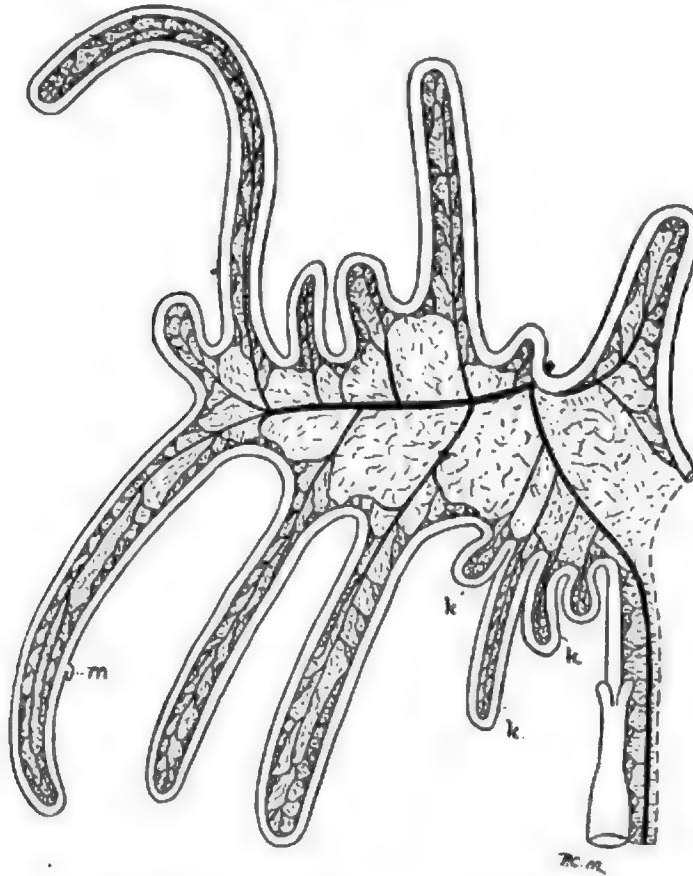
Of these I have had an opportunity of examining only the Northern Petrel and the Albatross. In *Fulmarus glacialis* (26. fig. 7) the duodenum is compound, and Meckel's tract is expanded into six very long, narrow and straight minor loops, the fourth of which bears Meckel's diverticulum, while the last is a distinct supra-duodenal loop drained by a "bridging" vein. The terminal portion of Meckel's tract is long, thrown into supra-cæcal kinks as in *Spheniscus* and the Eagles, and is drained by the posterior mesenteric vein. The cæca are vestigial, and the rectum is extremely short. In the Albatross, *Diomedea exulans* (fig. 9), the duodenum is simple, and Meckel's tract is drawn out into a series of extremely long narrow loops (the length of these is underestimated in the figure). The form of the tract is much alike in the Albatross and the Petrel; the chief difference is that the first three minor loops of the Petrel are represented in the Albatross by two long loops with shorter loops between them. A very long loop bearing the Meckel's diverticulum then follows in both; the lower portion of Meckel's tract, the supra-cæcal kinks drained by the rectal vein, the vestigial cæca, and the very short rectum are alike in each. The only striking difference is that there does not appear to be a definite supra-duodenal loop with "bridging" vein in *Diomedea*. The specimen I examined had been preserved for long in spirit, and possibly I may have overlooked a "bridging" vein, although I examined the region minutely for it.

It is plain that the Procellariiform birds present a markedly apocentric type of intestinal tract, the special characters being the transformation of the middle loop into a number of definitely-placed minor loops, the appearance of supra-cæcal kinks on the large posterior portion of Meckel's tract, drained by the rectal vein, the vestigial cæca, and the very short rectum.

Gadow (12) unites the Colymbiformes, Sphenisciformes, Procellariiformes, and extinct Ichthyornithes into a "Legion" under the name Colymbomorphæ. Concerning the intestinal tract of the extinct forms we have no information. The others have all moved out from the archecentric condition. Their apocentricity is first a relatively increased

length in association with the nature of their food, and certainly multiradial; second, Meckel's tract in all, while remaining nearly symmetrical, tends to be drawn out into a series of long, narrow, and straight loops, a feature which may give some clue to affinity;

Fig. 9.



Intestinal Tract of *Diomedea exulans*. Lettering as before.

third, the rectum in all is very short. The Colymbiformes are least modified; the Penguins and Petrels are more modified, the two latter showing degeneration of the cæca and certain peculiarities in the posterior portion of Meckel's tract, peculiarities repeated in Steganopodes and Falconiformes.

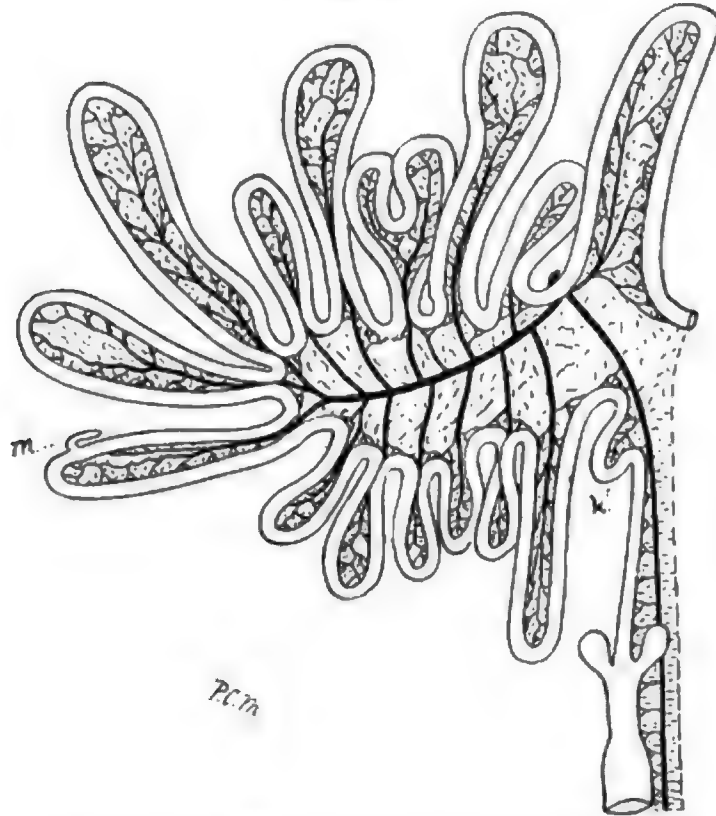
### CICONIIFORMES.

#### STEGANOPODES.

(1) PHAETHONTIDÆ.—*Phaethon* (fig. 10) displays a simple form of alimentary tract. The duodenal loop is simple; Meckel's tract is thrown into a series of narrow, minor loops, some of which are slightly complicated by folding. Meckel's diverticulum occurs on one of the minor loops rather more near the distal end of the tract. The posterior portion has no special supra-duodenal loop, and ends in a portion drained by the rectal or

posterior mesenteric vein and exhibiting a short supra-cæcal kink. The cæca are reduced, but not to the same extent as in other Steganopodes except the Pelicans. The rectum is extremely short. The three factors of the portal vein are of diagrammatic simplicity.

Fig. 10.

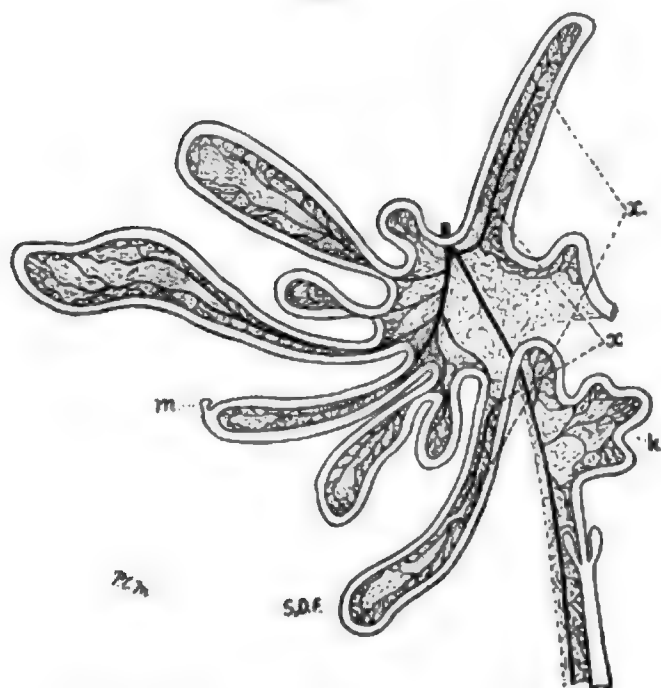
Intestinal Tract of *Phaethon flavirostris*. Lettering as before.

(2) **SULIDÆ.**—In *Sula bassana* (fig. 11) the apocentricity of *Phaethon* is carried further. The general arrangement is similar, but the duodenum is longer and is compound; certain of the minor loops of Meckel's tract are longer, especially the last, that forming a characteristic supra-duodenal loop with bridging vein; and the kink on the posterior part of Meckel's tract, that drained by the rectal vein, is larger.

(3) **PHALACROCORACIDÆ.**—In *Phalacrocorax carbo* (fig. 12) the duodenum is very long and narrow; Meckel's tract is extremely elongated, in which respect it resembles the condition found in *Platalea* and *Phœnicopterus*, and is symmetrically disposed about the middle mesenteric vein, which in the archecentric fashion runs from a large Meckel's diverticulum. The supra-duodenal loop is long; there is a large supra-cæcal kink supplied by the rectal vein. The cæca are vestigial, and the rectum is relatively longer than in *Phaethon* and *Sula*. In *Plotus anhinga* (fig. 13) the form of the tract presents marked differences. The duodenum is similar. The anterior portion of Meckel's tract is relatively much shorter, and consists of a single narrow loop, followed by one very

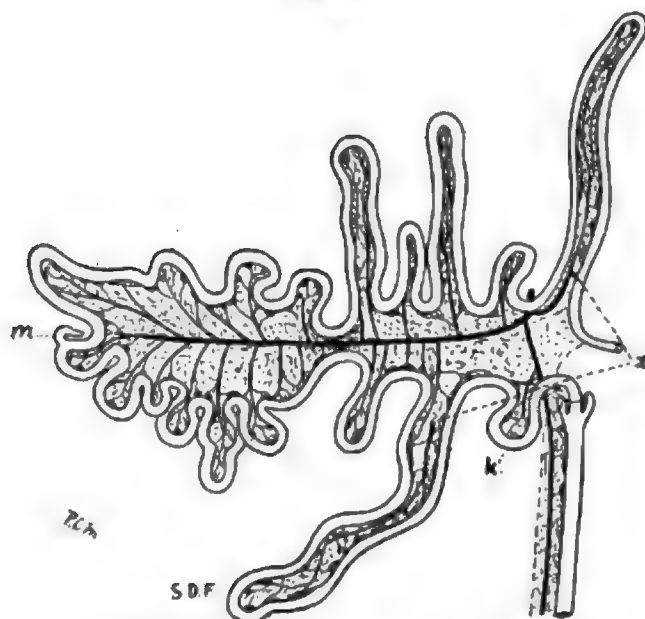


Fig. 11.



Intestinal Tract of *Sula bassana*. Lettering as before.

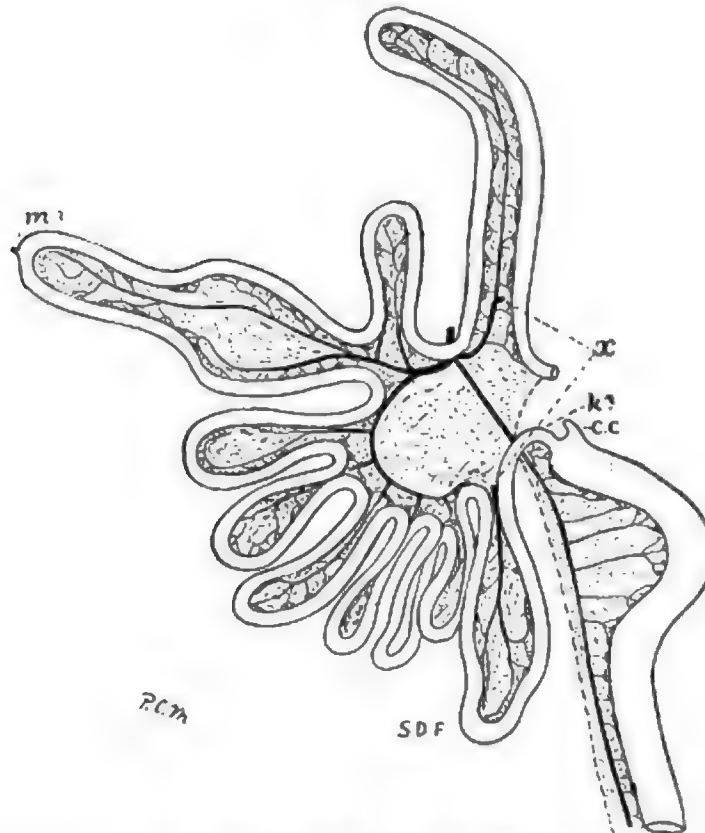
Fig. 12.



Intestinal Tract of *Phalacrocorax carbo*. Lettering as before.

long loop, at the end of which lay what I took to have been a Meckel's diverticulum. Then follows a very long posterior portion, relatively longer than in the diagram, and thrown into a series of straight minor folds, the posterior of which is a supra-duodenal loop with a "bridging" vein. Just beyond this is the trace of a supra-cæcal kink. The rectum is long and wide, in fact is typically archecentric. Of the usual pair of cæca, only one was developed, and that in a vestigial form, but Beddard (2) states that individuals vary, some possessing two vestiges. The minor loops of Meckel's tract show a

Fig. 13.

Intestinal Tract of *Plotus ankinga*.

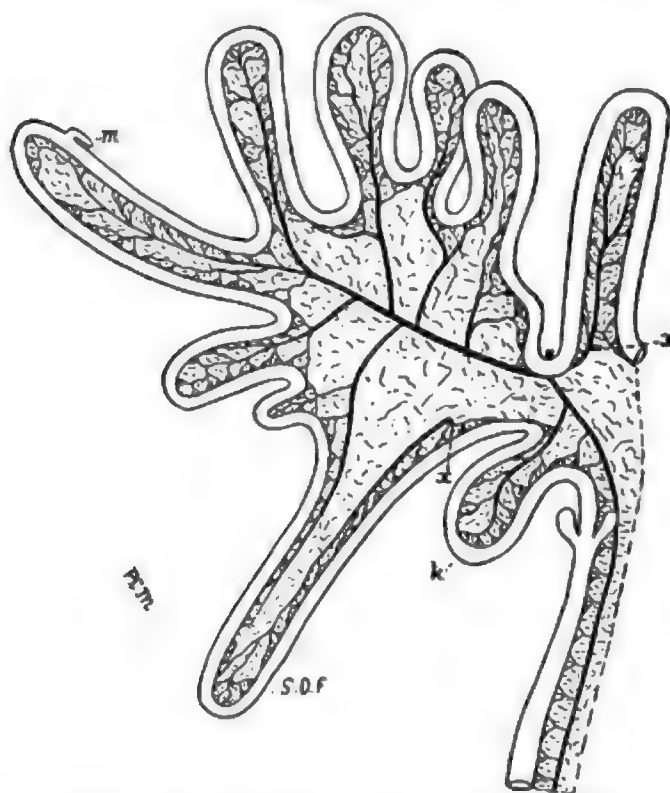
C.C., single colic caecum; k?, possible supra-cæcal kink; m?, possible position of Meckel's diverticulum.

tendency to be bunched up as in the Pelicans. If I were wrong in my placing of Meckel's diverticulum, and what I took for it was the merest trace, the character of the gut would not be so unlike that found in the Cormorant; but in any event the differences between the two forms are wide, and make it plain that if other characters justify the inclusion of *Plotus* among the Phalacrocoracidae, the association is by no means close. On the evidence of the intestinal tract I should be inclined to place *Plotus* in a separate family.

(4) FREGATIDÆ.—In *Fregata* (fig. 14) the form of the intestinal tract is very like that displayed by *Phaethon*. The chief differences are that in *Fregata* the whole tract is

relatively somewhat shorter, the minor expansions of Meckel's tract are less numerous, that bearing Meckel's diverticulum being longer; there is a supra-duodenal loop; the cæca are less developed and the rectum is longer.

Fig. 14.



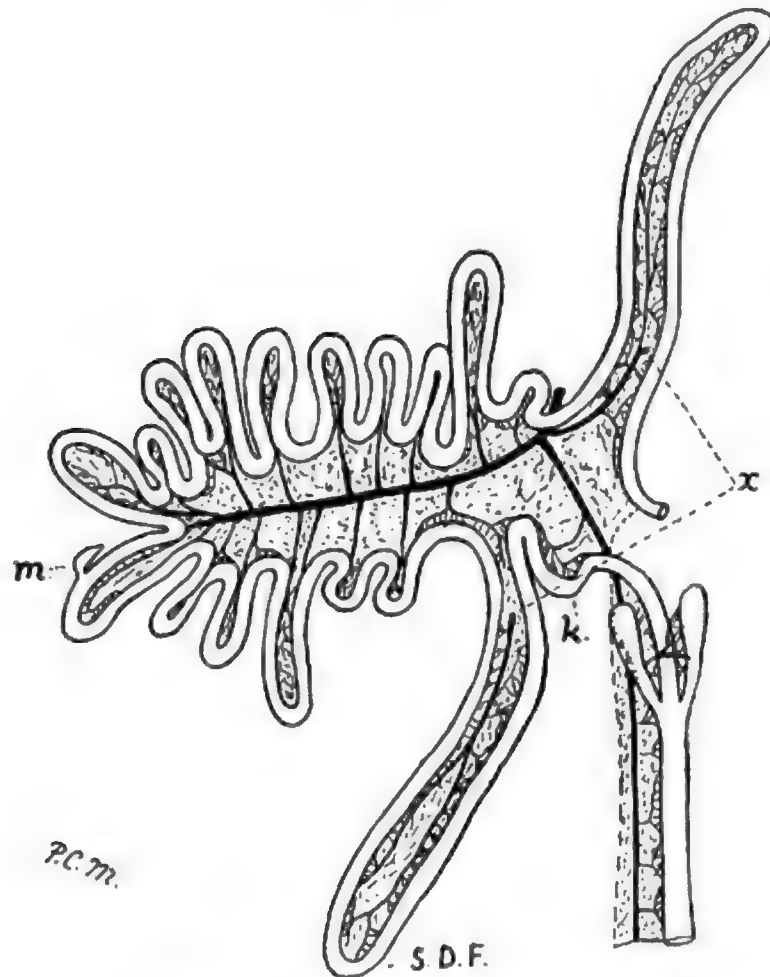
Intestinal Tract of a species of *Fregata*. Lettering as before.

(5) **PELECANIDÆ.**—In the Pelicans (*Pelecanus rufescens*, fig. 15) the form of the intestinal tract is simple. The duodenal loop is long, narrow, and somewhat twisted; Meckel's tract is nearly symmetrical round the middle mesenteric vein which runs from the position of a large Meckel's diverticulum. There is a well-formed supra-duodenal loop, a supra-cæcal kink drained by the rectal vein, and the cæca are relatively longer than in other Steganopodes. The minor loops of Meckel's tract tend to be bunched up towards the mesenteric vein, a feature that cannot well be represented in a diagram showing the unfolded condition.

The Steganopodes are typically piscivorous, although some of them also take any kind of floating carrion, and in all of them allowance must be made for the piscivorous length of gut. Their apocentricity, apart from such homoplasy, consists, as in the Colymbomorphæ, of a general tendency for Meckel's tract to be expanded into a series of short straight loops. In the Colymbomorphæ, however, these loops frequently increase in length and become reduced in number; in the Steganopodes the tendency is rather for the minor loops to increase in number, and for Meckel's tract to be either bunched up

tightly or much elongated as a whole. These two forms of modification of the middle loop point towards the condition found in many of the Ibiidæ such as *Platalea*, and in

Fig. 15.



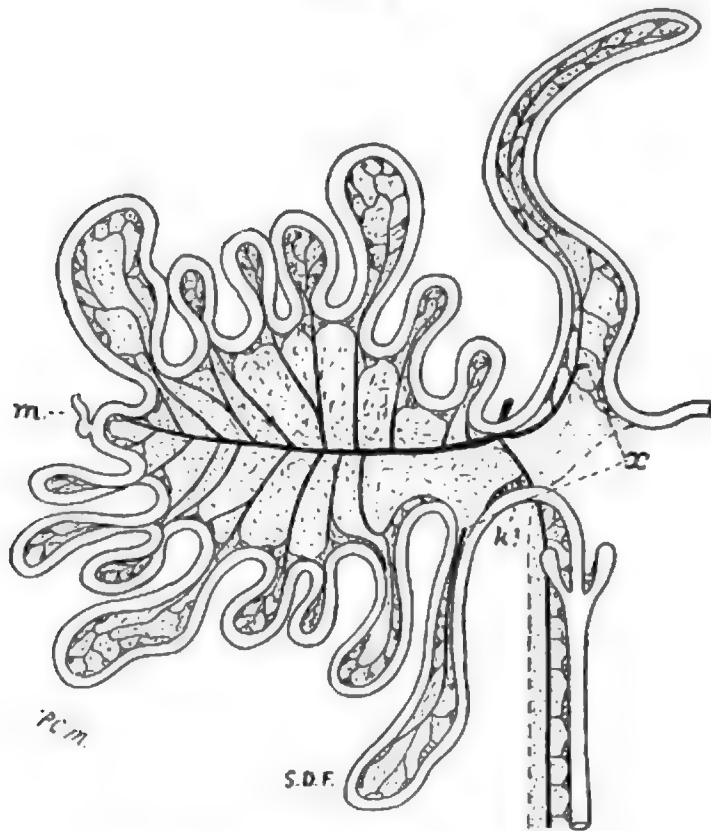
Intestinal Tract of *Pelicanus rufescens*. Lettering as before.

the Flamingoes, where Meckel's tract, in the unfolded condition not unlike that of the Pelican, is in life twisted irregularly into a spiral. I find, then, in the apocentricity of the Steganopod Meckel's tract an underlying resemblance to that of the Colymbomorphæ, as if a metacentric position had been common to all these, but from this metacentre the two sets have diverged in different directions. The reduction of the cæca, the shortening of the rectum, and the formation of minor loops above the cæca, but drained by the posterior mesenteric vein, are common, but not invariable, in the whole set.

ARDEÆ.

(1) SCOPIDÆ.—In *Scopus umbretta* (fig. 16) the duodenum is long and slightly twisted. Meckel's tract is nearly symmetrical, a large Meckel's diverticulum being near the centre of its periphery, and is expanded into a number of wide, irregular, but in the main straight minor loops, the last of these being longer and forming a typical supra-duodenal loop. The rectum is straight, of moderate length, and the pair of cæca are reduced. The veins are typical. A small area supplied by the rectal vein corresponds to the supra-cæcal kink.

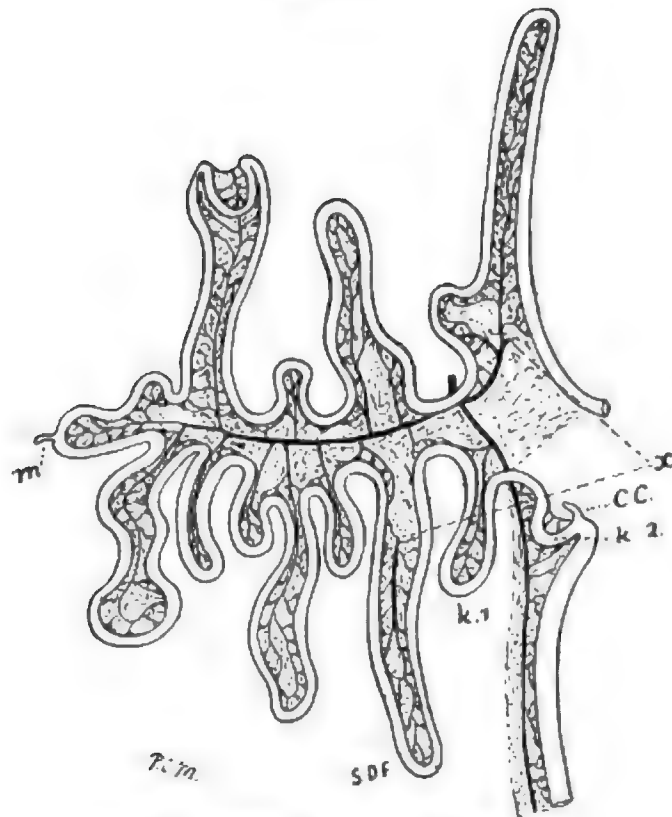
Fig. 16.



Intestinal Tract of *Scopus umbretta*. Lettering as before.

(2) ARDEIDÆ.—In the Herons and Bitterns, of which I have examined a number of species, the ground-form is like that in *Scopus*. The duodenum is a long narrow loop, nearly always considerably twisted to the left, usually more so than appears in the two figures (*Nycticorax griseus*, fig. 17, and *Ardea candidissima*, fig. 18). Meckel's tract may be rather elongated as in *Nycticorax*, or relatively shorter as in *Ardea*. It is always drawn out into a large number of minor loops, many of which are irregularly folded, and not infrequently complex in themselves; the distal minor loops in *Ardea* (fig. 18) show this in a relatively simple form. In the Little Bittern and some other

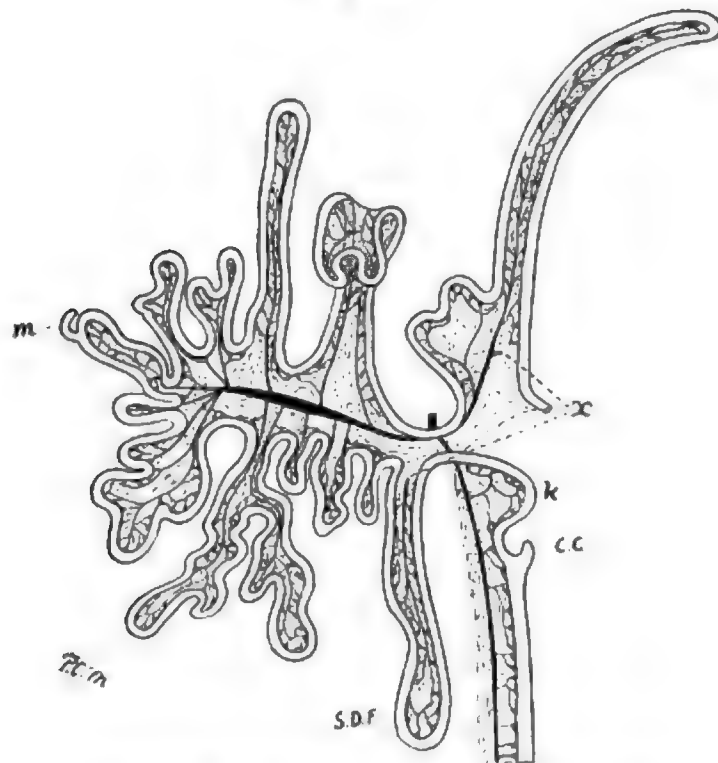
Fig. 17.



Intestinal Tract of *Nycticorax griseus*.

C.C., single colic caecum characteristic of Herons; k. 1 and k. 2, supra-caecal kinks. Other lettering as before.

Fig. 18.



Intestinal Tract of *Ardea candidissima*. Lettering as before.

Heron the complexity of the minor loops is very great. The penultimate loop of Meckel's tract is always a typical supra-duodenal loop with "bridging" vein, and then follows a supra-cæcal kink. It is typical of the Ardeidæ, as is well known, that one of the two colic cæca be absent, and I have found no exception to this, but Beddard has recorded such a case. The rectum itself is straight, but not very short.

A considerable part of the apocentricity of the intestinal tract in the Ardeæ must be attributed to the fact that they are relatively large birds with a diet consisting chiefly of fish, in consequence of which the gut is very long and narrow. Underlying this is a general resemblance to the ground-form of the Steganopod and Colymbomorph gut, shown in the symmetry of Meckel's tract around the middle mesenteric vein, the persistence of a large Meckel's diverticulum opposite the end of this vein, and the formation of a kink immediately above the colic cæca but supplied by the rectal vein. The special Ardeine features are the elongation of the duodenum as a narrow fold curving to the left; the throwing out of Meckel's tract into minor loops, which, straight in the simpler forms and always folded over simply ("orthocœly" of Gadow), tend to become complicated in themselves. The persistence of only one of the colic cæca is a most peculiar feature, normally absent only in *Scopus*. But the absence occurs not infrequently as an individual abnormality in some other birds, and I shall make further reference to such cases.

Although *Scopus*, so far as the character of the intestinal tract takes us, is more archcentric than the Herons and Bitterns, it plainly belongs to their group rather than to the Storks and Ibises.

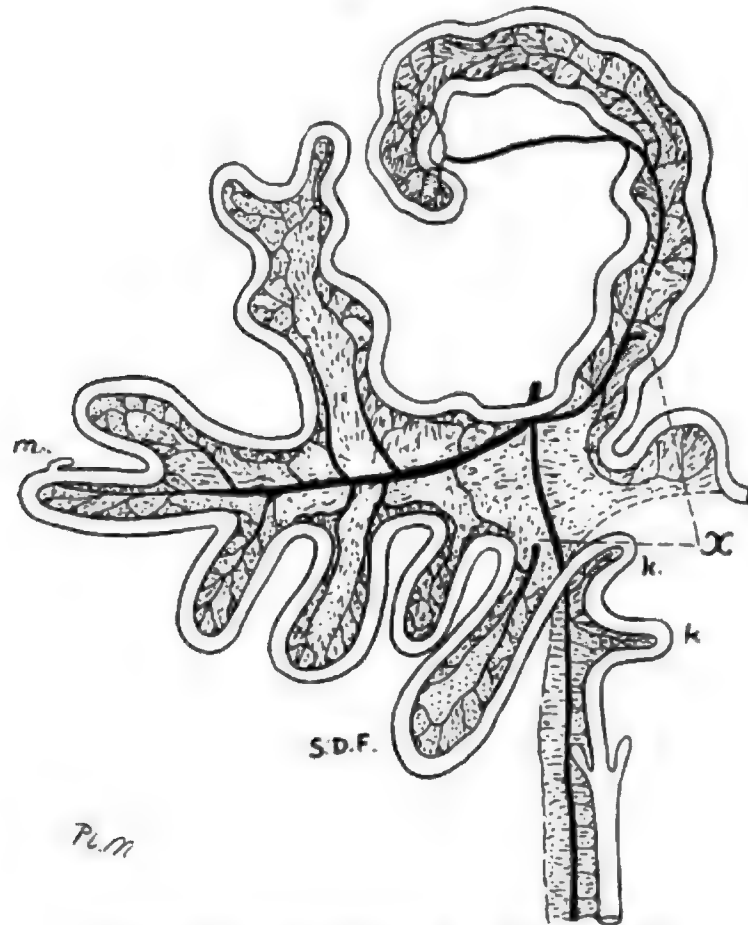
#### CICONIÆ.

(1) CICONIIDÆ.—The Storks, of which I have examined a considerable number, present a most interesting series of modifications. *Anastomus oscitans* (see Plate 21), the Indian Open-bill, displays so little difference from the ground-form of the intestinal tract among the set of birds I have been discussing, that I do not think it necessary to figure it in a separate block. The duodenum is short and straight; Meckel's tract is thrown into a very large number of short straight loops nearly symmetrically disposed around the middle mesenteric vein, the latter running backwards from a large Meckel's diverticulum. There is a very large and complicated supra-duodenal loop, more complicated than in any of the other Storks I have examined, but drained by the usual bridging vein. Above the reduced cæca lies a short kink drained by the rectal vein, and the rectum is straight and of moderate length. In *Pseudotantalus ibis* (fig. 19) the typical Ciconiine apocentricity begins to appear, and this is of the definite type that I call uniradial and am inclined to regard as a sure sign of affinity. The duodenum is enormously long, but the bending which appeared in Herons is here transformed to a spiral twist, represented in the figure as partially uncoiled, with the result that the vein is out of the mesentery. The first minor loop of Meckel's tract is very large and is in itself slightly twisted, and, in the unfolded state, partly rolled in the duodenal spiral. The remaining portion of Meckel's tract consists of a few simple folds, symmetrical



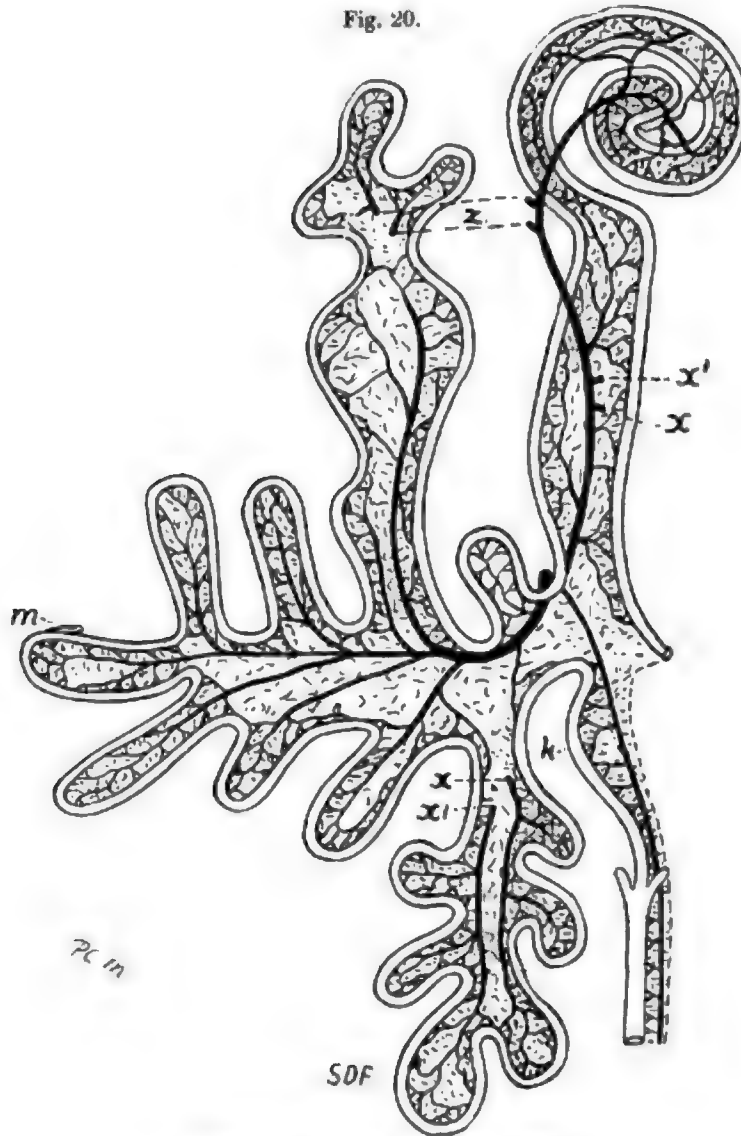
about the middle mesenteric vein, which runs from a Meckel's diverticulum. The distal portion of Meckel's tract forms first a distinct but short supra-duodenal loop, and then a double kink drained by the rectal vein. The cæca are reduced and the rectum is straight and short. *Dissura episcopus*, *Leptoptilus crumeniferus*, *L. argala*, and *Ciconia alba* are practically identical with this condition. In *Ciconia nigra*, which I have already figured (26. fig. 9), the condition is similar, except that the duodenal loop and the first

Fig. 19.

Intestinal Tract of *Pseudotantalus ibis*. Lettering as before.

loop of Meckel's tract form more perfect spirals, which in the unfolded condition are rolled together. In *Mycteria americana* (fig. 20) a similar condition exists, but the duodenal spiral and the spiral on the first loop of Meckel's tract are still longer and more complex, and are more intimately rolled together, with the result that certain factors of the duodenal vein run across draining the loop with which the duodenum is associated. These are represented in the figure as divided and the spirals are partly untwisted. Among the Storks, then, we see the interesting state of affairs that the character of the gut, starting from a metacentric position common to a large group of birds, develops along a special radius forming a uniradial line of apocentricity.

Fig. 20.



Intestinal Tract of *Mycteria americana*.

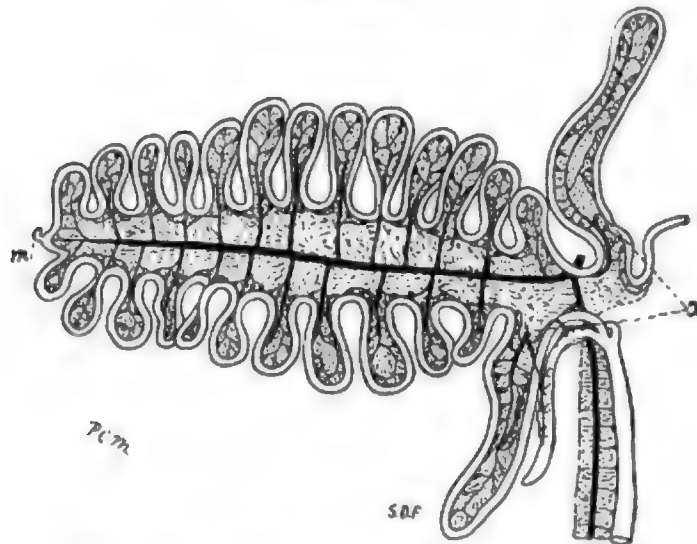
z, cut ends of veins from first loop of Meckel's Tract to duodenal vein.

(2) IBIDIDÆ.—I have already figured the intestinal tract of *Platalea leucorodia* (26. fig. 8). It is more archecentric than that found in other Ciconiiform birds. The duodenum is a long narrow loop bent round to the left as in the Herons, but showing no trace of spiral formation. Meckel's tract consists of an elongated system of short loops, symmetrically disposed round the middle mesenteric vein, which runs from a Meckel's diverticulum. This region of the gut is slightly twisted into a spiral in the unfolded condition. The last loop of Meckel's tract forms a simple supra-duodenal fold; the cæca are short, and the rectum is straight but considerably reduced. *Platalea* is certainly low down in the Ciconiiform scale, but none the less it displays the features of the group in a simple form, and is quite different in the character of the gut from *Numenius* (Plate 22), a low Charadriiform bird with which it has been compared.

## PHÆNICOPTERI.

PHÆNICOPTERIDÆ.—In *Phænicopterus ruber* (fig. 21) the duodenum is a simple loop, but with a slight Heron-like twist. Meckel's tract is very much elongated as in *Platalea*, and, again as in that bird, it consists of very many short loops symmetrical about the middle mesenteric vein which runs towards a Meckel's diverticulum. As in *Platalea* this region is twisted into a rude spiral, and there is a well-formed supra-duodenal loop. The cæca are long, and the rectum is of moderate length but straight. The only Anserine feature in the intestinal tract of the Flamingo is the presence of long cæca; and this, as we shall see in the further course of this memoir, is an obviously multiradial apocentricity. In all other respects the intestinal tract of the Flamingo is that of a low Ciconiiform bird.

Fig. 21.

Intestinal Tract of *Phænicopterus ruber*. Lettering as before.

It is unnecessary to do more than sum up in a few words the conditions of the gut found among the Ciconiiform birds. The ground-form is closely similar to that of the Colymbomorphæ, pointing towards the existence of a common metacentre for all these birds. From this metacentre the groups of Ciconiiformes have diverged in different directions and to different amounts. The Steganopods show a tendency to the bunching up of the loops of Meckel's tract on the axis given by the middle mesenteric vein. The Herons display a tendency to the individual elaboration of the minor loops of Meckel's tract. The Ciconiine birds show the most definitely uniradial apocentricity, consisting of an elaboration and intimate connection between the duodenum and the first loop of Meckel's tract, with a reduction of the posterior portion of Meckel's tract, except the supra-duodenal loop. The Ibididæ, or at least *Platalea*, show a primitive elaboration of Meckel's tract as a whole, and this tendency is carried further in the Flamingoes.

# ANSERIFORMES.

## PALAMEDEÆ.

**PALAMEDEIDÆ.**—I described the intestinal tract of *Palamedea* above (fig. 1). The intestinal tracts of *Chauna chavaria* (26. fig. 10) and of *C. derbiana* do not differ from that of *Palamedea* in any essential detail. I am following Dr. Gadow's classification for convenience of reference, but it is obvious that from the character of the intestines the Palamedeæ have no claim to be placed in close association with the other Anseriform birds, or indeed with any of the Carinate birds with which I have as yet been dealing. The Palamedeæ exhibit what I take to be the most primitive or archecentric type of intestinal tract to be found among birds. In the gut they have a general resemblance to the Ratites, and to the lowest members of all the other groups; to such they bear more resemblance than to the Ducks and Geese, which in the intestinal tract exhibit a definite or uniradial apocentricity, no trace of which occurs in any of the three Screamers. On the character of the intestinal tract alone I would not remove the Screamers from other birds, but rather all other birds from the Screamers, leaving them in central and primitive isolation.

## ANSERES.

**ANSERIDÆ.**—I have shown that in the Carinates I have up to this point discussed, with the exception of the Palamedeæ, there is strong evidence for the existence of the apocentric type of gut which forms a metacentre from which the various groups have diverged further. The metacentric character consists chiefly in the transformation of Meckel's tract into a definite series of narrow, straight loops, folded in the mode Gadow terms orthocœlous, and arranged nearly symmetrically round the middle mesenteric vein, which forms an axial line running from a Meckel's diverticulum. The form of the gut in the Anseridæ can be referred easily to such a metacentric condition. In *Anseranas melanoleuca* (fig. 22) this metacentric condition is reproduced with almost diagrammatic fidelity, an interesting circumstance in view of the primitive position among the Anseres generally assigned to this bird. The duodenum is a long narrow loop; Meckel's tract is thrown into very symmetrically-arranged narrow minor loops, the most peripheral of which bears a large Meckel's diverticulum. Between this and the duodenum there are three minor loops, a number typical of this part of the gut in the Anseres. The last loop of Meckel's tract is a typical supra-duodenal loop with the usual "bridging" vein from the duodenum, and with the very long cœca closely applied to it. The rectum is not very short but is straight. In *Cygnus atratus*, the tract of which I have figured in a former paper (26. fig. 11), certain modifications of the type in *Anseranas* are present. The first three minor loops of Meckel's tract are more complicated, showing a tendency to give off secondary loops. The axial loop, which bears Meckel's diverticulum, is greatly elongated and usually somewhat irregularly folded, with the result that the main vein leaves the mesentery, being shorter than the loop itself. The minor loop, just posterior

Fig. 22.

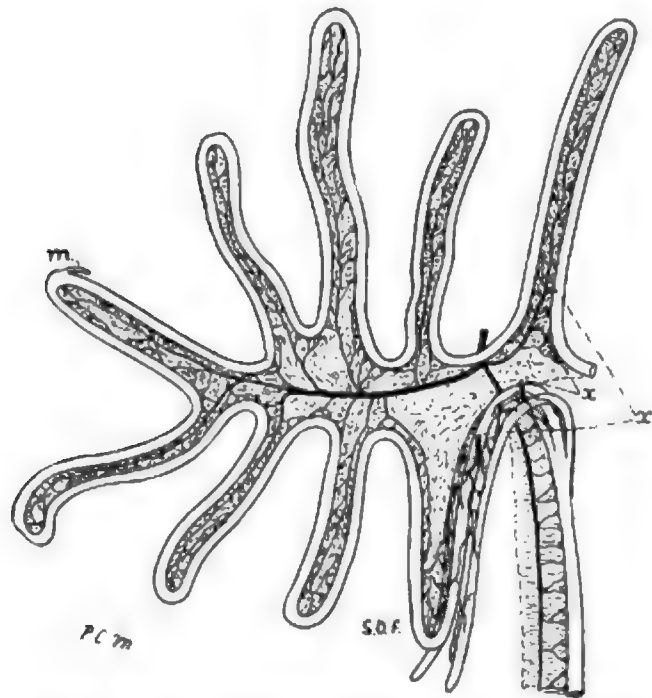
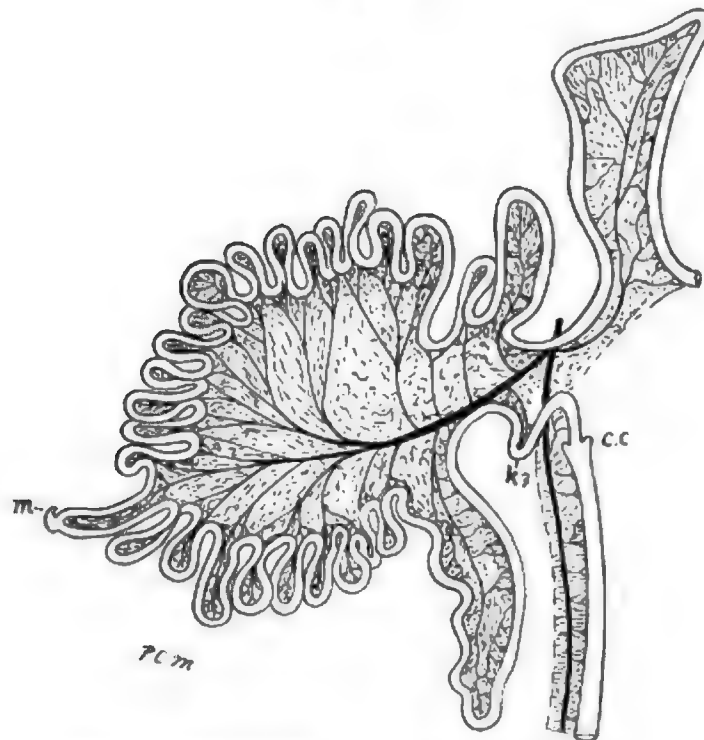
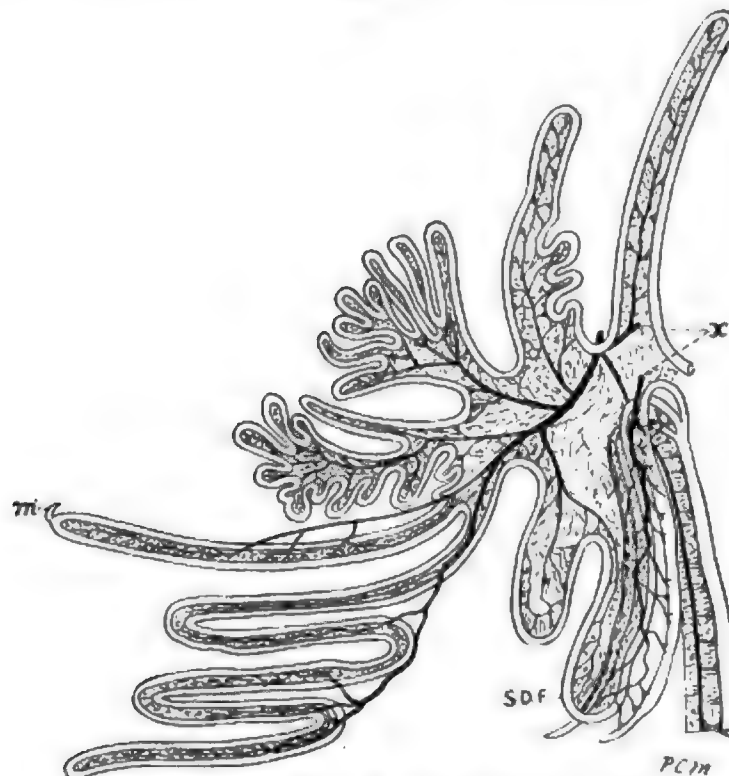
Intestinal Tract of *Anseranas melanoleuca*. Lettering as before.

Fig. 23.

Intestinal Tract of *Mergus albellus*. Lettering as before.

to this, is usually elongated and may be similarly twisted. The supra-duodenal loop, the cæca, and the rectum are as in *Anseranas*. The vast majority of Ducks and Geese that I have examined, however different their size and habits, faithfully reproduce this type. The diagram given for *Cygnus atratus*, with the most trifling alterations, might serve for *Anas*, *Anser*, *Æx*, *Chaulelasmus*, *Bernicla*, *Dendrocygna*, *Fuligula*, *Nesonetta*, *Tadorna*, and doubtless, so constant is the type, for many others. *Mergus albellus*, the Smew, presents an interesting variation (fig. 23). The duodenum is unusually wide; Meckel's tract is thrown into a large number of very short loops at the periphery of an almost circular mesenteric fold, but Meckel's diverticulum lies at the apex of a somewhat longer fold lying in the axis of the system. There is a supra-duodenal loop, but it is not

Fig. 24.

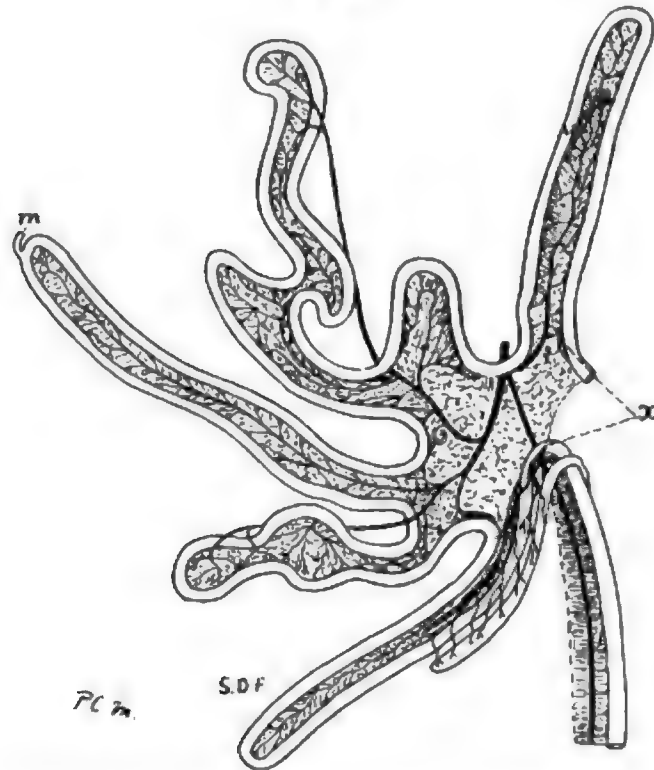


Intestinal Tract of *Spatula clypeata*. Lettering as before.

drained by a "bridging" vein. The colic cæca are paired, but practically non-existent, and Beddard (2. p. 459) mentions an instance where one of the two was absolutely non-existent. At first sight this intestinal tract appears more arche-centric than that of any of the other Anseriform birds except the Palamedæ, but I do not doubt that it is an instance of what I term pseudocentric simplicity. The cæca are obviously degenerate, and in other Mergansers they are longer; and examination of the first part of Meckel's tract shows that it might have been derived by a fusion of the three first minor loops, these having been more complicated than in *Cygnus*, and more as they are in *Spatula* (fig. 24). There is a short supra-cæcal kink, but it is not supplied by the rectal vein. *Spatula clypeata* (fig. 24) shows a form of gut which is simply a further elaboration of

the *Cygnus* type. The modifications are confined to Meckel's tract. The three most anterior minor loops of that region are complicated by an elaborate series of minor folds; the axial loop bearing Meckel's diverticulum is as in *Cygnus*, but the loop next posterior to that is enormously long and folded on itself, the vein having left the mesentery and running a much shorter course than the loop itself. In *Nettopus coromandelianus* (fig. 25) the gut is relatively shorter, and an apocentric simplification

Fig. 25.

Intestinal Tract of *Nettopus coromandelianus*. Lettering as before.

has taken place. The three proximal loops of Meckel's tract are represented by one short and then a very long loop, and the loop next distad of the axial loop is contorted. In these modified loops the veins leave the mesentery, a condition comparatively rare among birds, but very common in the Anseres.

Considering them from the point of view of the intestinal tract, it is plain that the other Anseriformes must be removed from the Palamedæ. The latter are archecentric. The former start from a metacentric position common to the Colymbomorphæ and the Ciconiiformes, but have diverged apocentrically from that position, forming a specially Anserine metacentre (Plate 22).

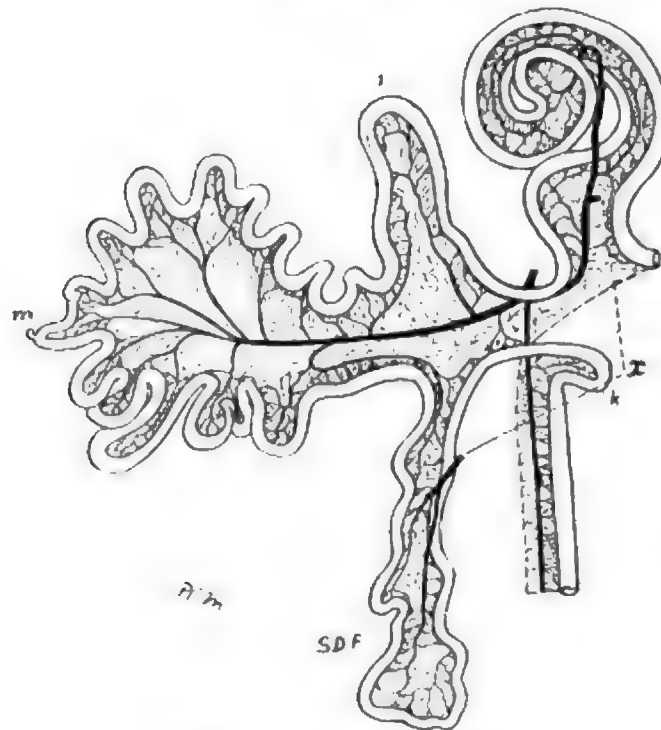


FALCONIFORMES.

CATHARTÆ.

CATHARTIDÆ.—Of these I have been able to examine only *Cathartes aura* (fig. 26). The duodenum is long and is coiled into an irregular spiral. Meckel's tract presents first one very wide loop and then a nearly circular expansion symmetrical about a Meckel's diverticulum and thrown into short irregular folds. Then follows a very large but

Fig. 26.



Intestinal Tract of *Cathartes aura*.

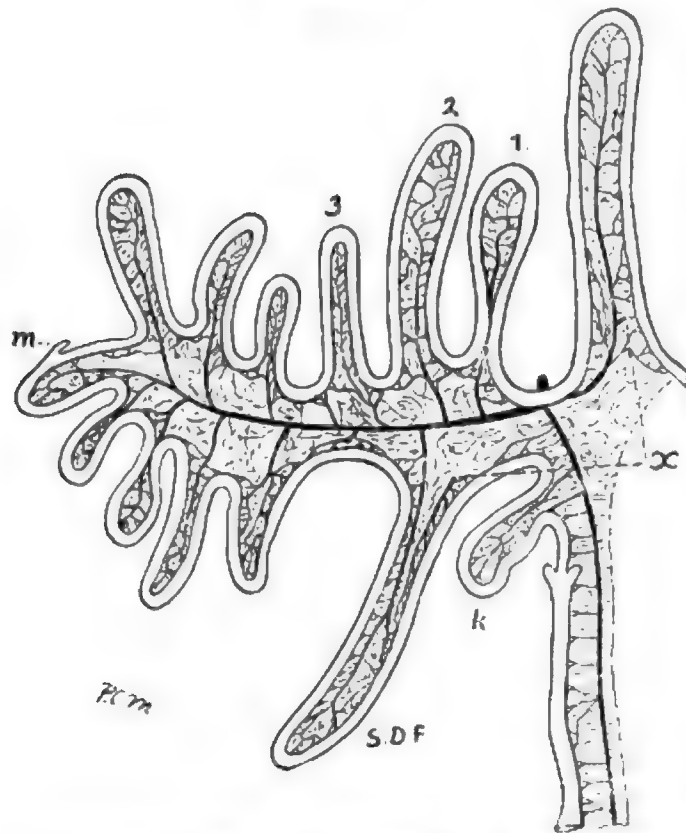
Lettering as before.

typical supra-duodenal loop with "bridging" vein. The cæca are totally absent, but immediately above their normal position lies the kink supplied by the rectal vein. I have already shown that this peculiar little loop is a recurring feature among the Carinates we have been considering. It occurs without exception in all the Falconiform birds.

## ACCIPITRES.

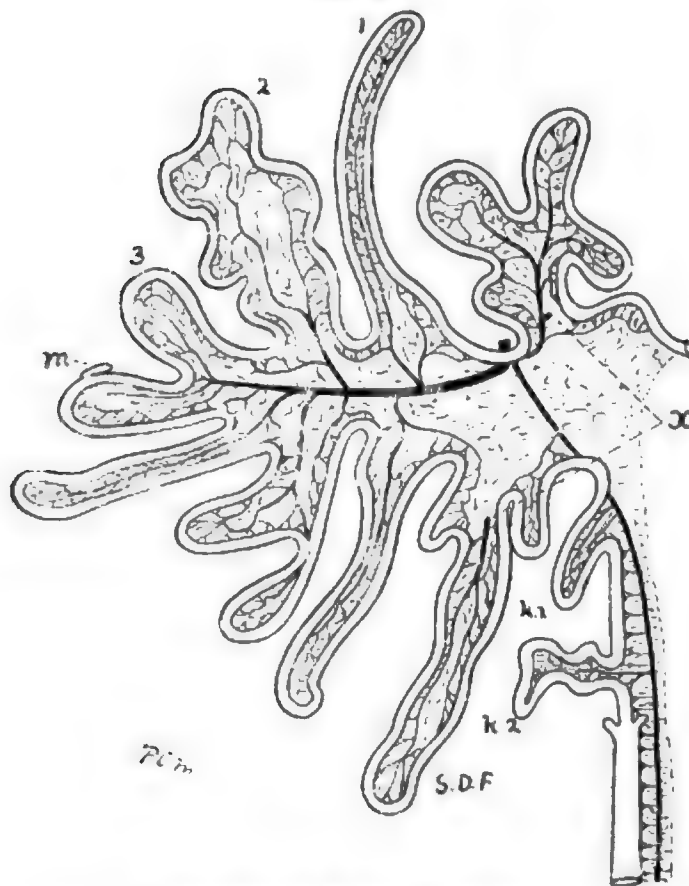
GYPOGERANIDÆ. — In *Serpentarius reptilivorus* (fig. 27) the duodenum is simple. Meckel's tract presents first three narrow minor folds, and then expands into a nearly circular portion like that in *Cathartes*, the axis being given by the middle mesenteric vein which runs from a Meckel's diverticulum. Then follows a long supra-duodenal loop, drained partially by a "bridging" vein. Posterior to this is a typical supra-cæcal kink, and then a pair of reduced cæca. The rectum is of moderate length and straight.

Fig. 27.

Intestinal Tract of *Serpentarius reptilivorus*. Lettering as before.

VULTURIDÆ. — *Neophron percnopterus* (fig. 28) and other Vultures which I have examined are closely similar. The duodenum is an irregularly expanded loop. Meckel's tract presents three distinct minor loops (numbered 1, 2, and 3 in the figure), which reappear constantly in Falconiform birds; then follows an axial loop bearing Meckel's diverticulum, and then several long, rather irregular loops, the last of which is a typical supra-duodenal loop with "bridging" vein. The cæca are vestigial, and above them lie two supra-cæcal kinks drained by the rectal vein. The rectum is short and straight.

Fig. 28.



Intestinal Tract of *Neophron percnopterus*.  
1, 2, 3, three anterior loops of Meckel's Tract. Other lettering as before.

#### FALCONIDÆ.

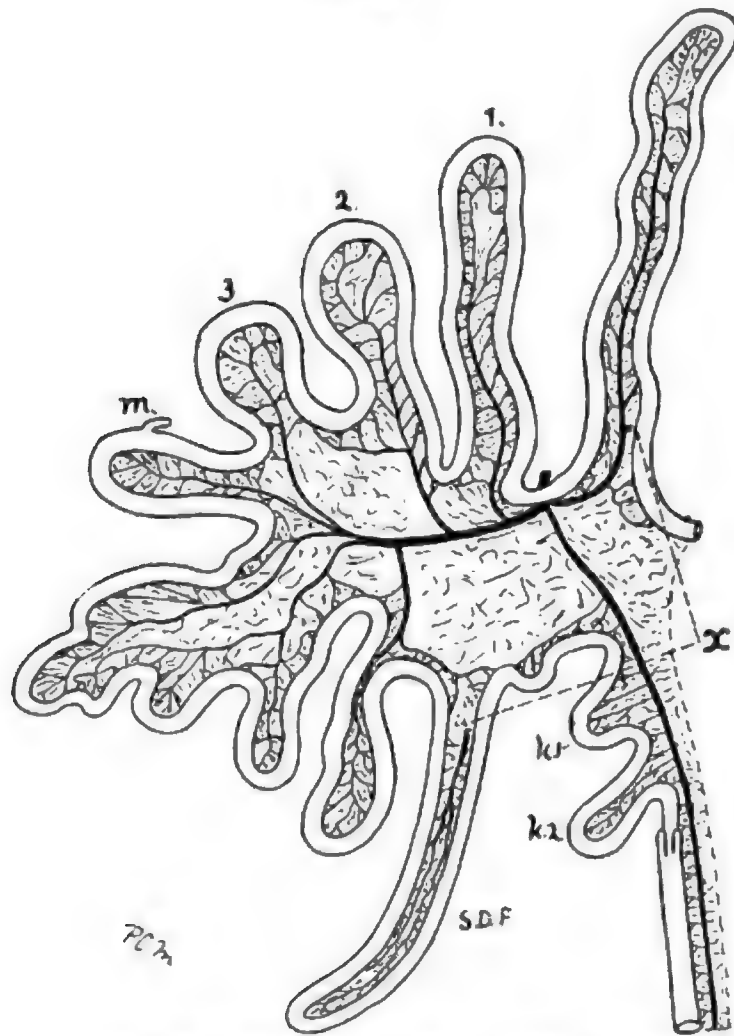
(1) *Gypætinæ*.—*Gypohierax angolensis* (fig. 29) displays an alimentary tract extremely like that of the true Vultures. The duodenum is simpler, being a long, narrow loop. Meckel's tract begins with three distinct minor loops (1, 2, and 3); then follows an axial loop, with Meckel's diverticulum, and the remaining part of the tract, including the supra-caecal kinks and the vestigial cæca, is precisely as in the Vultures.

(2) *Polyborinæ*.—In *Polyborus brasiliensis* (fig. 30), the Brazilian Caracara, the duodenum forms a long, narrow loop, which is wound into a spiral. Meckel's tract consists of a set of small loops arranged very symmetrically, the axial loop as usual bearing a Meckel's diverticulum. There is a well-formed but single supra-caecal kink in the normal position, and anterior to that a supra-duodenal loop. The cæca are vestigial, and the rectum is short and straight.

(3) *Accipitrinæ*.—In *Circus cineraceus* (fig. 31) is to be found what may be regarded as a central condition for the Falconidæ. The duodenum is a large, very wide loop.

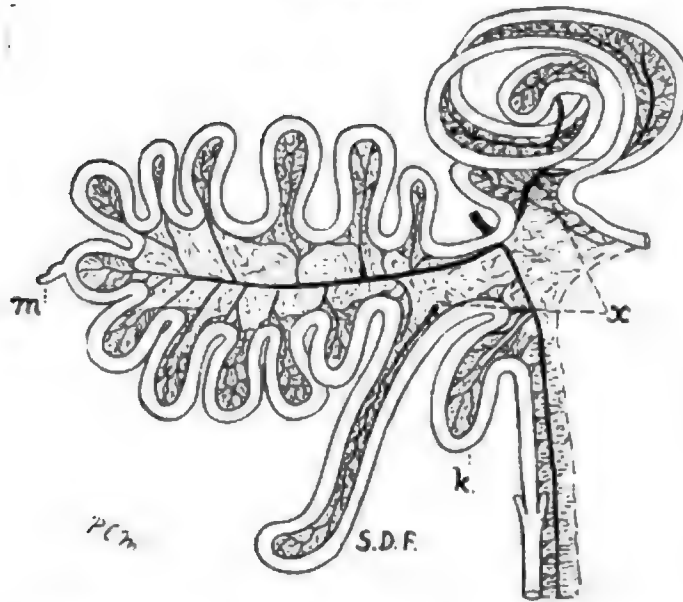
Meckel's tract exhibits first three distinct minor loops, and then is prolonged axially, bearing at its extremity a Meckel's diverticulum. The posterior part of the tract has one or two minor loops and a large supra-duodenal loop with two "bridging" veins. Then comes a large supra-cæcal kink. The cæca are vestigial, and the rectum is short and straight. Another *Circus* (the species of which was not identified), *Circaëtus gallicus*, and *Helotarsus ecaudatus* all exhibited precisely the same conformation.

Fig. 29.

Intestinal Tract of *Gypohierax angolensis*. Lettering as before.

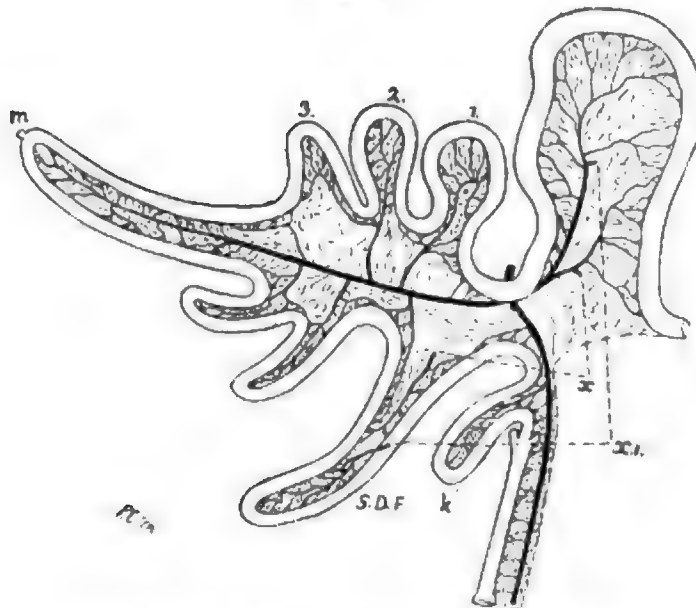
(4) *Aquilinae*.—I have examined *Aquila audax*, *A. chrysaëtus*, *A. Perreuxi*, *Morphnus guianensis*, *Spizaëtus coronatus*, and *Haliaëtus albicilla* and *H. leucogaster*. I have already described the conformation of the gut in the White-tailed Sea-Eagle (26. fig. 12). The duodenum is very long, being thrown into a complicated system of secondary folds. Meckel's tract, also, is much elongated and its greater part is composed of a series of short irregular loops suspended at the periphery of an oval stretch of mesentery, the apex

Fig. 30.



Intestinal Tract of *Polyborus brasiliensis*. Lettering as before.

Fig. 31.



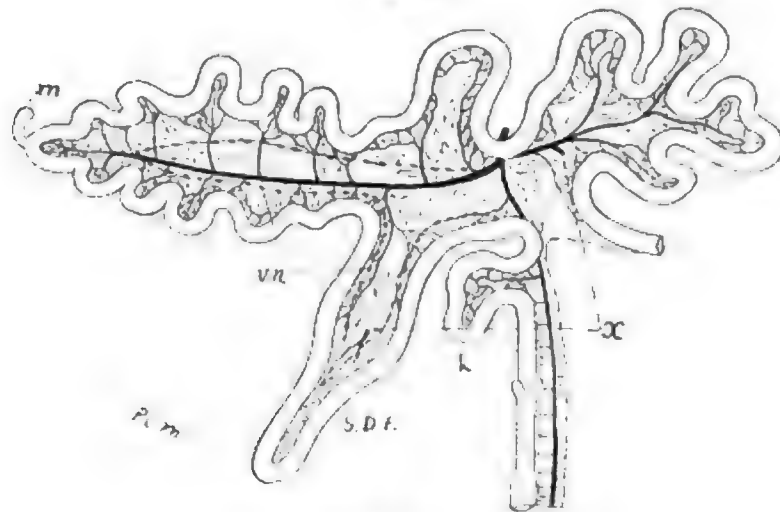
Intestinal Tract of *Circus cineraceus*. Lettering as before.

of the system carrying a Meckel's diverticulum. There is a well-formed supra-duodenal loop, which is spirally twisted, and a large supra-cæcal kink has a similar arrangement. The cæca are vestigial, and the rectum is short and straight. *Haliaëtus leucogaster* differs from the foregoing only in that its duodenum is spirally twisted. These two birds are large and chiefly piscivorous, and the homoplastic increase in gut-length has obscured the peculiar characters of the Falconiform gut, but the general symmetry, the peculiar duodenums, and the well-formed supra-cæcal kinks are sufficiently distinctive. The other Aquilinæ repeat exactly the pattern displayed by *Circus*, the only slight modification I have found being that the supra-duodenal loop in *Spizaëtus*, although drained by a "bridging" vein, is very small. The supra-cæcal kink is very large in most and distinct in all.

(5) *Buteoninæ*.—Of these I have examined *Astur tachiro*, *Asturina magnirostris*, *Buteo erythronotus*, *B. ferox*, *B. jacob*, *Milvus forinda*, *M. iclinus*, *M. migrans*. In all the pattern of *Circus* is reproduced with close fidelity. The duodenum is irregular, sometimes long, narrow, and straight as in the genus *Buteo*, sometimes irregularly expanded, or folded upon itself several times as in some species of *Milvus*. Meckel's tract is always as in *Circus*, save that in a *Buteo* no trace of Meckel's diverticulum was retained. The supra-duodenal fold is always present as also is a large supra-cæcal kink. The cæca are vestigial and the rectum is short and straight.

(6) *Falconinæ*.—I have examined *Falco concolor*, *F. Feldeggii*, *F. lunarius*, *F. melanogenys*, *F. peregrinus*, and *Microhierax melanoleucus*. The Falconinæ certainly exhibit

Fig. 32.

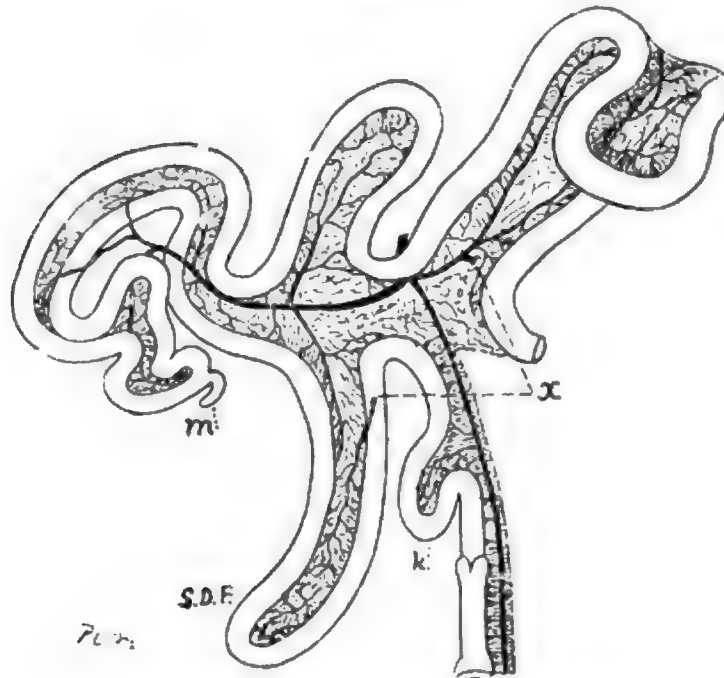
Intestinal Tract of *Falco melanogenys*.

v.n., visceral nerve-chain. Lettering as before.

the most specialized or apocentric form of gut among the Falconidæ. The duodenum is always a large irregular loop, sometimes with minor folds (fig. 32), sometimes bent on itself (fig. 33). Meckel's tract is always very much elongated in the axial line, and

invariably bears at its apex an unusually large Meckel's diverticulum. In many Falcons the first portion of Meckel's tract displays the three minor loops which recur among Falconiform birds. In *Falco melanogenys* (fig. 32) and *F. Feldeggii* (fig. 33) two of these have disappeared, probably in connection with the very great elongation of the tract as a whole. The apical portion of Meckel's tract may be irregularly twisted as in the

Fig. 33.



Intestinal Tract of *Falco Feldeggii*. Lettering as before.

Peregrine Falcon and in *Falco melanogenys* (fig. 32), or it may be coiled into an irregular spiral, an apocentric peculiarity found in many specialized types, for instance in Pigeons and Passerines. There is always a supra-duodenal loop and a supra-cæcal kink. The cæca are vestigial; in a Peregrine Falcon I found only one present. The rectum is short and straight.

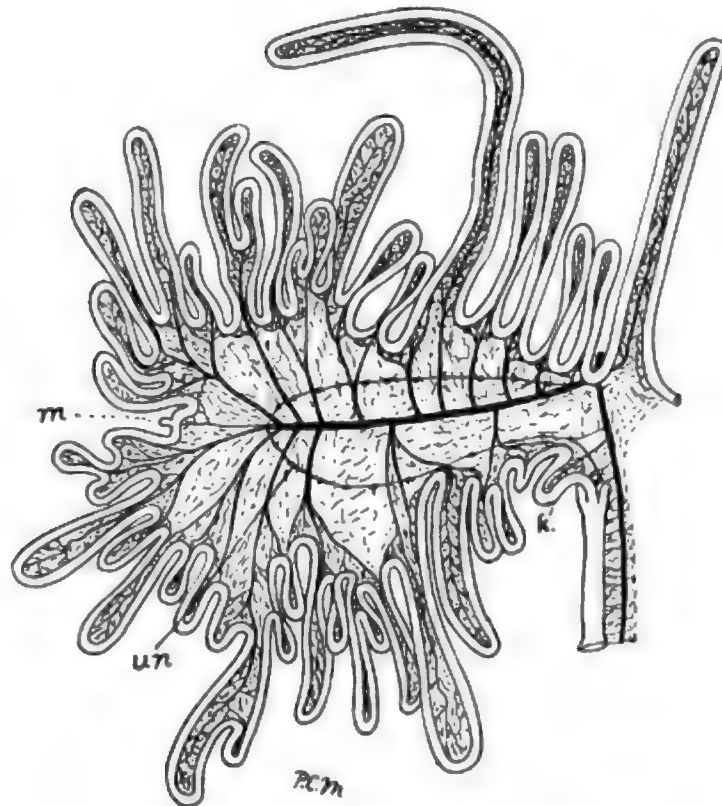
**PANDIONIDÆ.**—In the Osprey, *Pandion haliaëtus* (fig. 34), the gut is enormously long, and is of very narrow calibre, a modification obviously in association with piscivorous habit. The duodenum is long and narrow. Meckel's tract is thrown into a very large number of narrow loops, arranged round a nearly circular mesenteric expanse, the diverticulum being in the usual place at the central point of the curved system. There is no supra-duodenal loop, but there is a small supra-cæcal kink. The cæca are vestigial and the rectum is short and straight.

The Falconiformes are on the average rather large birds with diet in the main carnivorous, with some exceptions which are piscivorous, and a few which live on insects. Except in the piscivorous cases, there is little correction to be made for diet.



The carnivorous forms are on the average the larger, and the carnivorous shortening of the gut is in consequence disguised by the relative increase in length associated with size. The general features of the group are a tendency for the duodenum to be irregular, enlarged, very long, or spirally twisted; for Meckel's tract to exhibit three definite minor loops anterior to a median loop bearing a Meckel's diverticulum, and, posteriorly to that, first one or two irregular loops and then a supra-duodenal loop and at least one supra-cecal kink drained by the rectal vein; the cæca are always vestigial and the rectum short and straight. The departures from this common type are—first, the irregularities in the fish-eaters; second, a progressive tendency for the lengthening of Meckel's tract

Fig. 34.

Intestinal Tract of *Pandion haliaetus*. Lettering as before.

in the axial line with consequent obliteration of one or more of the other minor loops, and, in the most apocentric cases, with a spiral folding of the tract; third, *Serpentarius* shows distad of the first three loops of Meckel's tract a circular expansion of the mesentery bearing a number of minor loops, and this condition leads naturally to the condition in *Cathartes*, where the circular expansion involves the second and third of the definite loops on the proximal side of Meckel's tract. Attempts have been made to show a more intimate relation between the *Cathartæ* and some of the *Ciconiiform* birds than between these and other *Falconiformes*; there is no ground for such a conclusion in the structure of the intestinal tract. Still less ground is there for attempting to place in intimate

relation any of the Falconiformes with *Cariama*. The latter bird, as will appear later, is definitely a member of the Gruiform assemblage, and for relations between the Gruiform birds and the Falconiform birds it is necessary, so far as the characters of the intestinal tract take us, to go back to the archecentric type underlying all birds.

SUMMARY OF THE PELARGO-COLYMBOMORPHINE BRIGADE. (Plate 21.)

At this point it is convenient to attempt a *résumé* of the conclusions to which study of the Intestinal Tract has so far led.

Taking the form in *Palamedea* as the archecentric type, it appears that the Struthious birds are grouped indifferently around it, as they all display the archecentric character in an unmodified or very slightly modified form. Of the Colymbomorphæ, *Colymbus* exhibits the simplest type, in fact a slight but definite modification of the *Palamedea* form, consisting in the expansion of Meckel's tract into a set of straight, narrow loops, one of which is axial and bears the diverticulum, the others being arranged nearly symmetrically about the middle mesenteric vein. There is usually a supra-duodenal loop; the cæca are functional and the rectum is short and straight. This form is of great importance, as it is a Pelargo-Colymbomorphine metacentre from which radiate the type of intestinal tract displayed by Gadow's first Brigade of birds, including the Legion Colymbomorphæ with the Colymbiformes, the Sphenisciformes, and the Procellariiformes, and the Legion Pelargomorphæ with the Ciconiiformes, Anseriformes, and Falconiformes. The Grebes are more apocentric modifications of this metacentric type, the change being chiefly a reduction of the number of loops of Meckel's tract with a corresponding increase in the length of the individual loops. A slight but still more apocentric modification of the Pelargo-Colymbomorphine metacentre produces a new central position, which may be called the Steganopod metacentre. The two chief additional characters of this are, firstly, a tendency to complication and lengthening of the duodenum, a tendency which in nearly every case is actually fulfilled; and secondly, the appearance immediately above the cæca of a kink supplied by the rectal vessel, although belonging to the drainage-area of the middle mesenteric vein. Meckel's tract does not differ fundamentally (fig. 35) from the condition in the Pelargo-Colymbomorphine metacentre, but the cæca are reduced. The Sphenisciformes are modified from such a condition only by the greater length of their gut and consequent increase in the number of minor loops on Meckel's tract. The Procellariiformes are modified from it chiefly in the reduction of the number of loops on Meckel's tract and the great increase in length of the individual loops, the axial of which may be spirally twisted in the most apocentric forms, *e. g.*, the Oceanitidæ. Of the Ciconiiformes, the Steganopods retain their metacentric position. The Ardeæ start from that position (*Scopus*), but in the Ardeidæ the minor loops of Meckel's tract become very complicated and one of the two cæca is lost. The Ciconii start from the Steganopod metacentre with forms like *Anastomus*, but they rapidly reach a more apocentric condition, the chief peculiarity of which is the spiral twisting not only of the duodenum but of the first minor loop of Meckel's tract, and the twisting of these two spirals together, so that sometimes the blood-vessels are in

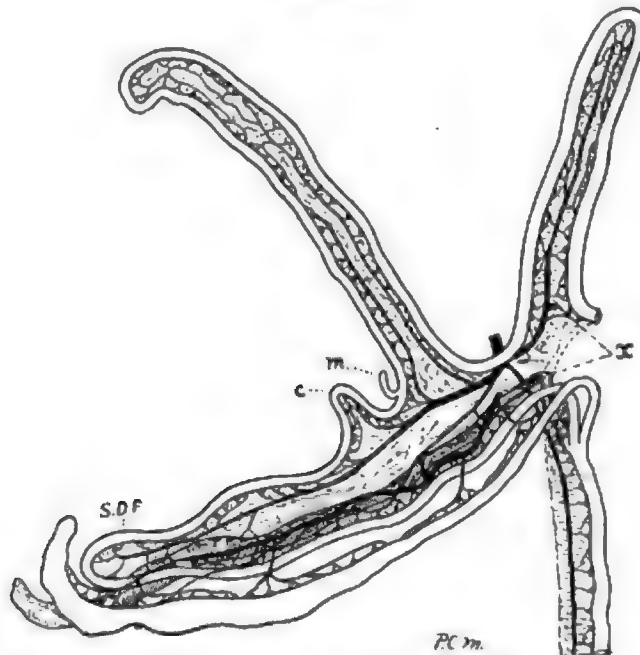


completely lost the cæca. *Pandion* stands by itself; its gut is so extremely long that none of the usual minor loops except the supra-cæcal kink can be identified. *Haliaeetus* is a simple modification of the Falconiform metacentre, the irregularity being due to increase in length. For the Anseridæ it is necessary to go back to the Pelargo-Colymbomorphine metacentre. *Anseranas* is practically in that position unmodified, save that the cæca are still longer, a condition common to all the Anseridæ except some of the Mergansers. The *Cygnus* type, with its three definite and contorted minor loops on the anterior portion of Meckel's tract and its very long axial loop with peculiar blood-vessels, gives an Anserine metacentre from which *Nettopus* and *Spatula* have diverged still further. *Mergus* is probably a pseudocentric modification of the *Spatula* type.

### TINAMIFORMES.

CRYPTURIDÆ.—Of these I have been able to examine the intestinal tract of several specimens of *Rhynchotus rufescens* and *Nothura maculosa*. The conformation is practically identical in these two forms. The duodenum is a long narrow loop; Meckel's tract (*Rhynchotus rufescens*, fig. 36) is divided into two nearly equal parts, the large

Fig. 36.



Intestinal Tract of *Rhynchotus rufescens*.

c, compare loop similarly marked in Gruiformes, figs. 41, 42, 43, &c. Other lettering as before.

Meckel's diverticulum lying between the two. The first portion is one very long narrow loop; the second portion is an equally long and narrow supra-duodenal loop drained by a branch of the middle mesenteric vein as well as by the usual "bridging" factor from the duodenal vein. Meckel's diverticulum was very large in two specimens of *Rhynchotus*, small in a third, and very small in *Nothura*. The small minor loop just distad of it

represented in figure 36 was present in two specimens of *Rhynchotus*, absent in another, and present in *Nothura*. The cæca were long in all, and Beddard (2) has notified the presence of long cæca in the other genera and species, and of very peculiar cæca in *Calodromas*. The rectum is short and straight.

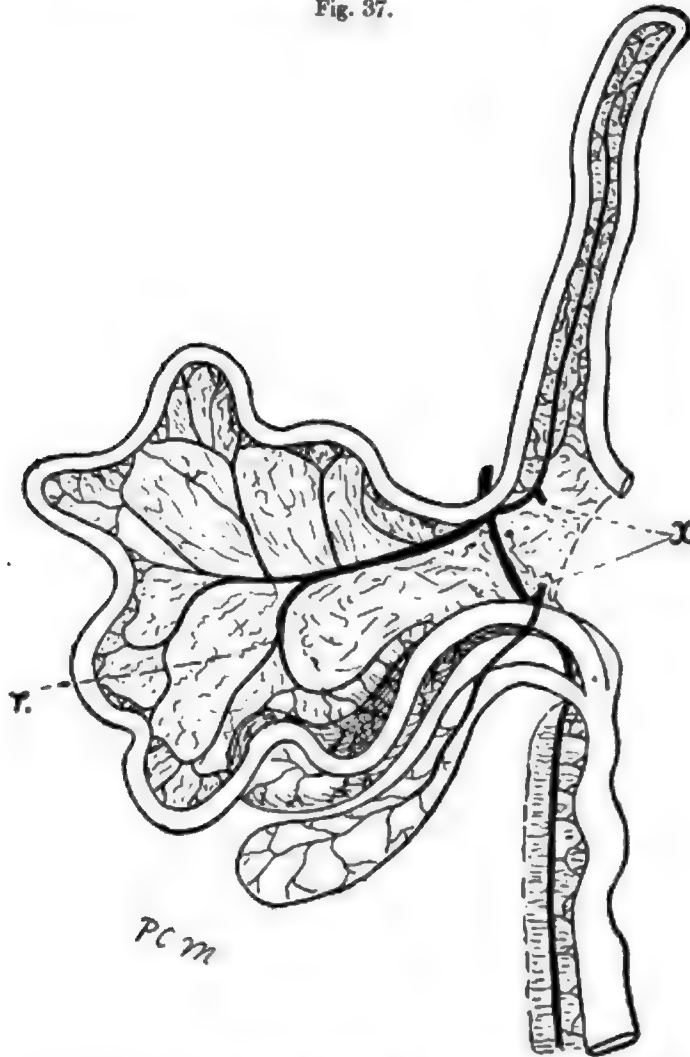
The figure may be taken as representing the morphological character of the Tract in the Tinamus, as there is little correction to be made for habits, and as the conformation is practically identical in relatively large forms such as *Rhynchotus*, and relatively small forms such as *Nothura*. It is clear, then, that the type of the intestinal tract in the Tinamiformes is markedly apocentric, and differs from the archecentric type of *Palamedea* and of the *Struthious* birds in that the rectum is straight, and more notably in that Meckel's tract is expanded into two long, straight, and narrow loops, one anterior, the other posterior to the rudiment of the yolk-sac, both being orthocoelous. Naturally, as the Ratites have intestinal tracts of archecentric conformation, it is as possible that the Tinamiform gut may be derived from the Ratite gut as from that of any other archecentric form. But so far as the character of the intestinal tract goes, there is no reason to associate the Tinamus specially with the Ratites. Nor is there any reason to associate the Tinamus in this matter with the Galliformes, for in these the gut shows a fundamental archecentricity underlying a tendency to apocentric development in the direction of expansion of that part of Meckel's tract supplied by the recurrent branch of the middle mesenteric vein, and there is no trace of this feature in the Tinamus. The gut of the Tinamus bears a close resemblance to that of specialized Ralline forms such as *Otis* (fig. 45). The gut of *Otis*, as I shall show later, can be regarded without difficulty as an apocentric derivative of that of less specialized Ralline forms, and for this reason the resemblance between it and the Tinamu may be merely superficial. There is, however, another reason for not rejecting the Ralline affinities of the Tinamiform gut too readily. As I shall explain later, I have only gone a little way in study of the autonomic nervous system, and therefore cannot yet weigh the value of evidence to be drawn from the modifications exhibited in different birds. There are, however, at least two strongly contrasting types. In one of these the visceral nerve of Meckel's tract forms a ganglionated chain which follows the contour of the gut. This type occurs in *Palamedea* (fig. 1, *v.n.*), in the *Struthious* birds, and in the Galliformes. In the other type there are a much smaller number of larger ganglia on the visceral nerve (*Otis*, fig. 45, *v.n.*). This type occurs in some of the Ralline birds and in at least *Nothura*. Another striking resemblance is that between the conformation of the gut in the Tinamus and in *Opisthocomus*. To this I shall recur later. The conformation of the gut, then, supports those who, like Gadow, isolate the Tinamus as Tinamiformes, but at the same time suggests possible relationships with Gruiform birds and with *Opisthocomus*.

#### GALLIFORMES.

MESITES.—I have no information regarding this group. Naturally knowledge of the conformation of the alimentary tract is much to be desired in the case of a bird the affinities of which are doubtful.

TURNICES.—In the Turnices (I have not seen *Pedionomus*) the duodenum (*Turnix Dussumieri*, fig. 37) is a long, narrow loop; Meckel's tract is suspended at the periphery of a nearly circular mesenteric expansion and bears no trace of the diverticulum. There is no specially formed supra-duodenal loop, but the very large cæca (which are dilated towards their extremities) are drained partly by a bridging vein from the duodenal vein. The rectum is relatively long and very slightly expanded into folds.

Fig. 37.



Intestinal Tract of *Turnix Dussumieri*.

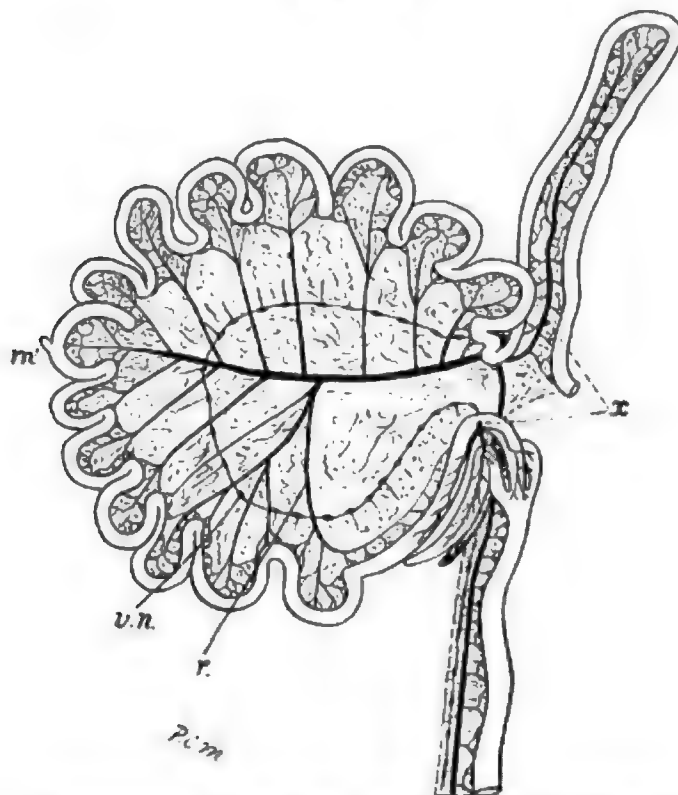
*r.*, recurrent factor of middle mesenteric vein. Other lettering as before.

This intestinal tract is markedly archecentric. The simple character and the arrangement of the blood-vessels are closely similar to the condition of *Palamedea*. The chief modifications are absence of the Meckel's diverticulum, the increased length of the cæca, and the relatively shorter rectum. So far as the character of the gut indicates systematic position, there is no reason either to retain *Turnix* among the Galliformes or to remove it from that assemblage. It is simply an archecentric form.

## GALLI.

**MEGAPODIDÆ.**—In *Talegallus Latham* (fig. 38) the duodenum is a straight, narrow loop of moderate length. Meckel's tract is swung at the periphery of an expanse of the mesentery, and forms almost a complete circle of which the middle mesenteric vein, running from the Meckel's diverticulum, forms a diameter; for the greater part of its

Fig. 38.

Intestinal Tract of *Talegallus Latham*. Lettering as before.

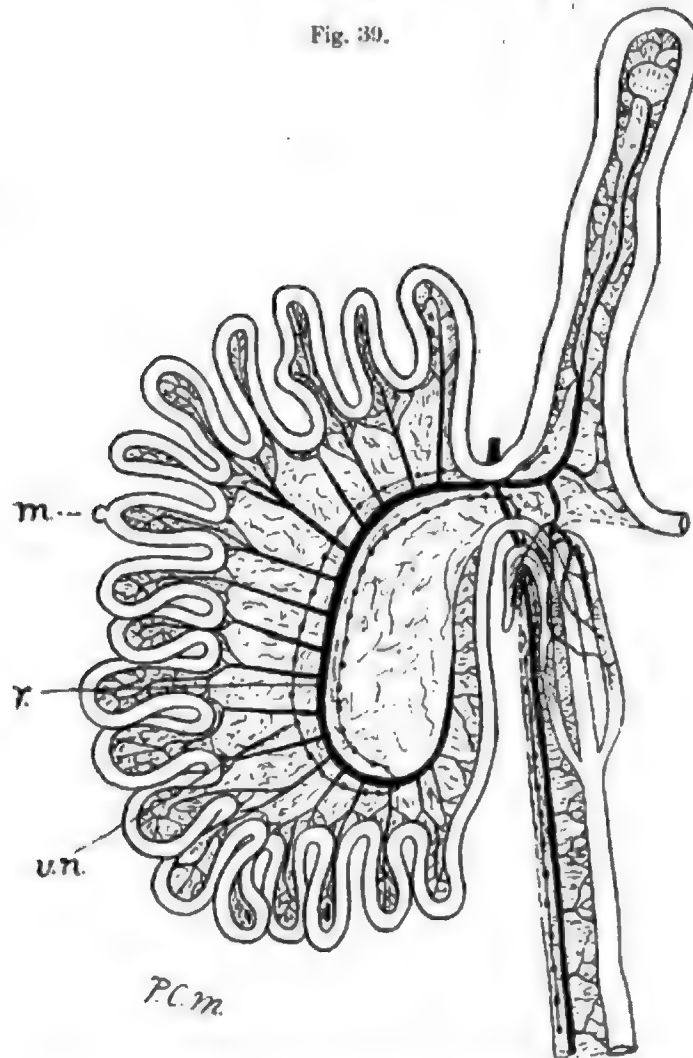
course this tract is thrown into very regular corrugations, but its distal portion is nearly straight. The recurrent factor of the middle mesenteric vein supplies a considerable part of Meckel's tract. The caeca are of moderate length and are drained partly by a "bridging" vein, and the rectum is fairly long and very slightly thrown into folds. A striking feature in *Talegallus*, as in other Galli, is the conspicuous visceral nerve (v.n.), which in this bird is a ganglionated chain following the sweep of Meckel's tract.

**CRACIDÆ.**—In *Crax Daubentoni* (fig. 39) the only notable difference from *Talegallus* in the formation of the gut relates to Meckel's tract. This area is much elongated distally, with the result that the recurrent factor of the middle mesenteric vein (r.) which supplies the distal portion of the tract is much enlarged, and appears to be the direct continuation of the middle mesenteric. That vein, however, in the embryo runs out as usual to the diverticulum as I figured in the case of *Argus giganteus* (26. fig. 2), and its real termination in the adult is one of the minor branches of the main blood-channel.



In association with the growth of the posterior portion of Meckel's tract, the visceral ganglionated chain forms a curious elongated loop, which, on comparison of figs. 38 and 39, will be seen to be obviously connected with the distal growth of the tract. In two other species of *Crax* and in two species of *Penelope* the conformation of the gut with its blood-vessels and nerve was identical in all main points with the condition just described.

Fig. 39.



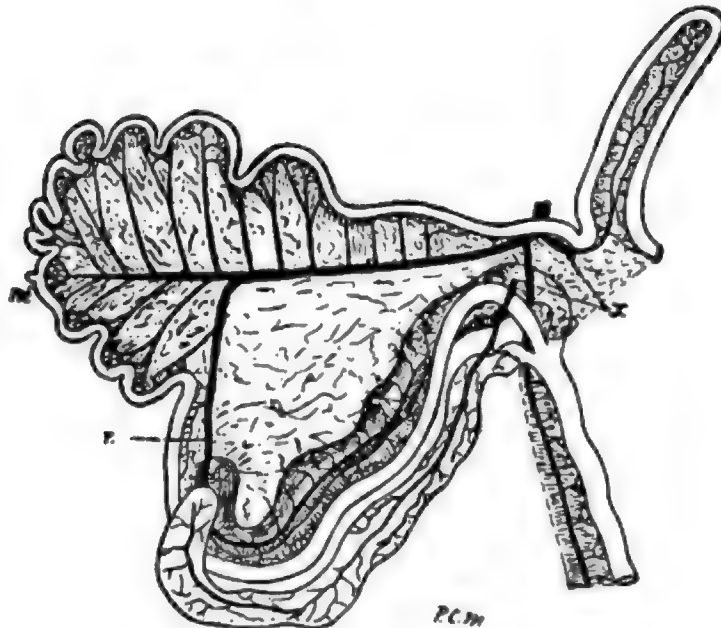
Intestinal Tract of *Crax Daubentoni*. Lettering as before.

GALLIDÆ.—I have examined a considerable number of these, including species of *Argus*, *Cucubis*, *Callipepla*, *Coturnix*, *Francolinus*, *Gallus*, *Lophophorus*, *Pavo*, *Phasianus*, *Perdix*, and *Tetrao*, and in all the conformation closely resembles that shown in the figure of *Pavo cristatus* (fig. 40). Meckel's tract is more elongated in the axial line than in the Cracidæ, and the middle mesenteric vein runs obviously from the remains of the diverticulum. There is a similar distal prolongation of the tract drained by a large recurrent vein, and to the straight distal portion of this the very

large cæca are closely applied, and are drained partly by the recurrent vein and partly by a "bridging" vein. The rectum is relatively short and straight.

In the Galli generally the only homoplastic cause of apocentricity that has to be allowed for is the increased length in the larger forms, and this is not sufficiently great to distort the morphological pattern of the intestinal coils. In all, the general character is markedly archecentric; in the Megapodidæ the archecentricity is most definite. In the Cracidæ there is an apocentric modification of a definite nature, although not great, and consisting in the peculiar expansion of the distal region of Meckel's tract with

Fig. 40.

Intestinal Tract of *Pavo cristatus*. Lettering as before.

coincident alteration of the visceral nerve and of the factors of the middle mesenteric vein. In the Gallidæ a similar change has occurred, but has affected the blood-vessels and the visceral nerve (the course of the latter, not indicated in the figure, very closely resembles that in *Talegallus*) to a much smaller amount. On the other hand, the cæca in the Gallidæ are much larger, and the small factor of the duodenal vein, which in *Crax* runs from them within the mesentery, is enlarged in the Gallidæ and has broken through the mesentery. It is plain that, so far as the conformation of the intestine indicates, the Galli are all closely allied, but there is a distinct basis for their division into Megapodidæ, Cracidæ, and Gallidæ.

#### OPISTHOCOMI.

I have already described and figured the intestinal tract of *Opisthocomus cristatus* (27. fig. 1). The duodenal loop is short and wide. Meckel's tract is thrown into three well-marked narrow loops, the second of which is rather wider and has a tendency to be twisted into a very slight spiral. In a chick and in two adults I found no trace of

Meckel's diverticulum, but towards the extremity of this loop the place of attachment of the yolk-sac was marked by a strong remnant of a ventral mesentery. In a third adult this mesentery ran to a very small vestige of Meckel's diverticulum. The most distal loop of Meckel's tract was wide, and closely applied to it were the pair of large cæca, drained partly by a "bridging" factor of the duodenal vein. The rectum is unusually long, retaining the archecentric condition of being thrown into minor folds.

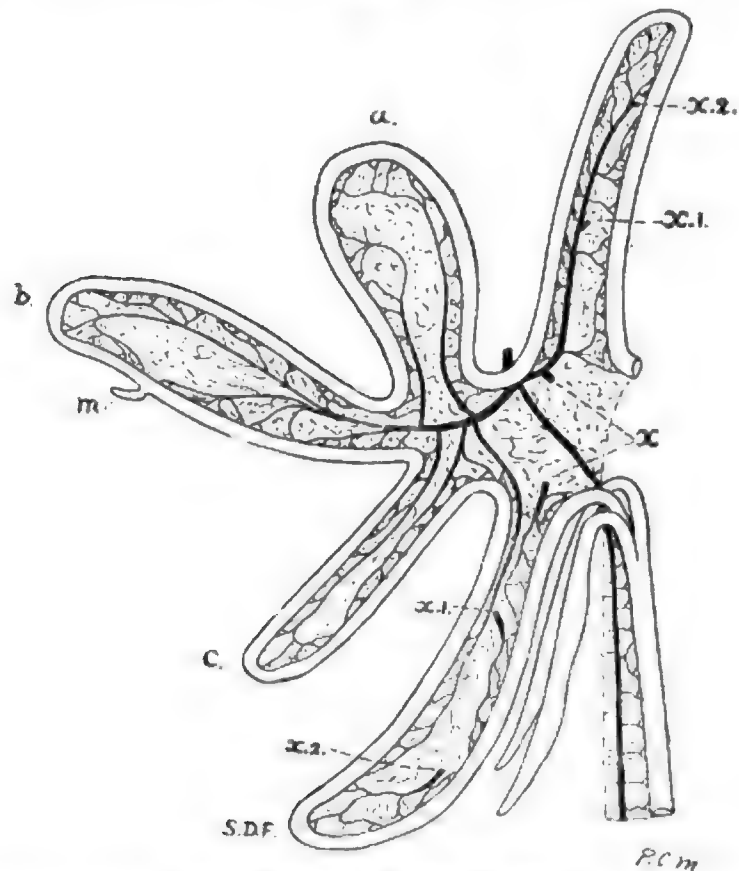
It is plain that the condition of the intestinal tract in this group is markedly apocentric, except with regard to the rectum. From this point of view the *Opisthocomi* do not find a natural place among the Galliformes—first, because in these latter the general condition of the gut is archecentric; and second, and more important, the small degree of apocentricity displayed among some of them consists of a peculiar expansion of the distal portion of Meckel's tract, and there is no trace of this feature in *Opisthocomus*. The apocentricity of *Opisthocomus* may be compared first with that of the Tinamus. If the very small loop seen just distal to Meckel's diverticulum in *Rhynchotus* (fig. 36) were prolonged, carrying with it the diverticulum, the condition in *Opisthocomus* would be reached. A second suggestion of relationship is, as I have already pointed out, given by comparison with the form of the tract in *Pterocles* and the Pigeons. In *Pterocles* (26. fig. 18) the condition of Meckel's tract and of the long cæca is extremely like that in *Opisthocomus*, the most notable difference being that in *Opisthocomus* the axial loop bearing the diverticulum is slightly twisted. In the Pigeons (26. fig. 19) the twisting of the axial loop may be carried much further and the cæca are reduced. When I first made this comparison of the gut in these three groups, I accepted the common view that eutaxy or quintocubitalism was a primitive condition, and diastaxy or aquintocubitalism a derived condition, and it was with hesitation that I put *Opisthocomus*, an eutaxic form, between *Pterocles*, a diastataxic form, and the Columbidae, then believed to be diastataxic. Since then I have shown that the eutaxic condition is probably a multiradial apocentricity derived independently from the diastataxic, archecentric condition of the wing. Moreover, I have shown (28) that among the Columbidae eutaxic forms occur. There is therefore no difficulty in the way of supposing that the gut forms in the Pigeons and in *Opisthocomus* are derivatives of the condition in *Pterocles*. In the paper in which I described the intestinal tract of *Opisthocomus* (27) I pointed out also that there were resemblances between the gut of *Opisthocomus* and the gut of the Cuculidae, thereby recalling Garrod's (13) suggested relationship between Fowls, *Opisthocomus*, and Cuculidae. It is true that among the Cuculidae Meckel's tract is thrown into three loops, but an examination of a larger number of Cuculidae has shown me that important differences distinguish the three loops in *Opisthocomus* and the loops in Cuculidae.

Taking the Galliformes as a whole, it appears that the form of the gut in the Turnices is archecentric; in the Galli it is still archecentric, but with a tendency to a special mode of apocentricity; in the *Opisthocomi* it is markedly apocentric, and the apocentricity is quite different in kind from that found among the Galli, but with marked resemblances to the condition in *Pterocles* and the Pigeons.

## GRUIFORMES.

**RALLIDÆ.**—In *Ocydromus australis* (fig. 41) what I find to be the typical Ralline conformation of the intestinal tract is presented. The duodenum is a straight, narrow loop of moderate length. Meckel's tract is drawn out into a definite number of loops, all of which are fairly straight. The first of these, marked "a" in the figures, succeeds the duodenum; the second ("b" in the figures) is axial and bears on its distal side a large Meckel's diverticulum. The third, marked "c," like the others is a narrow loop belonging to the drainage of the middle mesenteric vein; and the fourth is a well-marked supra-duodenal loop drained by more than one bridging factor of the duodenal vein. The

Fig. 41.

Intestinal Tract of *Ocydromus australis*.

a, b, c, the three loops of Meckel's Tract characteristic of the Gruiformes. Other lettering as before.

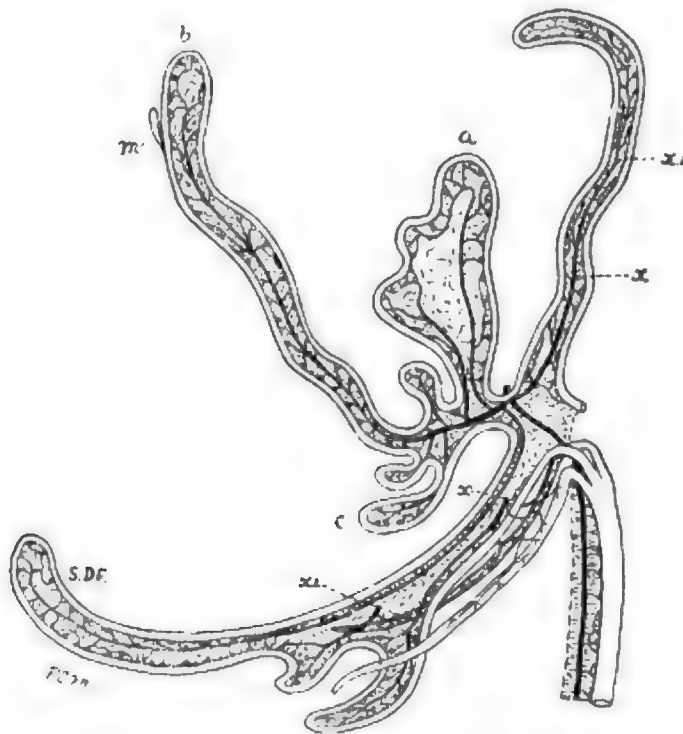
long caeca are closely attached to this last loop of Meckel's tract. The rectum is straight and of moderate length. This conformation is found in all the members of the Rallidæ that I have examined, e. g., *Aramides ypecaha*, *Crax pratensis*, *Gallinula phænicura*, *Ionornis martinicus*, *Porphyrio cæruleus*, and *P. poliocephalus*. I described this condition of the gut correctly in a former paper, but in the drawing of *Crax* (26. fig. 13) the third minor loop has been omitted by an unfortunate mistake, so that the description does not

tally with the figure. The differences which occur among the Rallidæ are insignificant ; in some, there are two "bridging" veins, in some, one ; the Meckel's diverticulum, which is always large, may be extremely large, the size of this structure being a characteristic feature of the group ; the third subsidiary loop of Meckel's tract occasionally is relatively smaller than the other loops.

GRUIDÆ.

(1) *Gruinæ*.—In *Grus virgo* (fig. 42) and other species of *Grus*, and species of *Anthropoides* and *Balcarica* are practically identical, the large size has brought with it a relatively great increase of length, but the fundamental identity of the conformation of the gut with that exhibited by the Rails is obvious. The duodenum is similar,

Fig. 42.



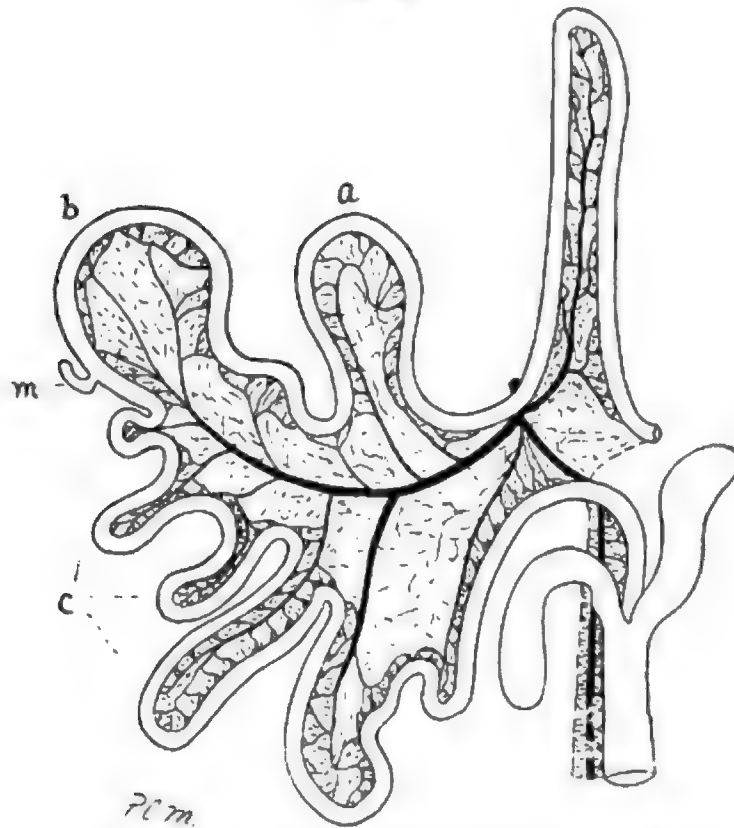
Intestinal Tract of *Grus virgo*. Lettering as in fig. 41.

although, on account of its great length, it is partly bent. Meckel's tract displays the same four loops : "a" being widened out ; "b," the axial loop being very long but carrying a Meckel's diverticulum in the characteristic position, on the distal limb of the loop ; "c" being small but compound ; and the supra-duodenal loop to which the long caeca are attached being much enlarged. It is plain that we have here a simple modification of the Ralline pattern, the modification being due to the relatively greater length of gut that occurs in larger birds.

(2) *Araminæ*.—The very interesting form *Aramus scolopaceus* (fig. 43) displays a conformation of the intestinal tract which differs only in minor respects from that in the

Rails and Cranes. The duodenum is normal; Meckel's tract displays the loops which I have marked "a" and "b" precisely as in the Rails, and "b" the axial loop bears a large diverticulum on its distal limb. The posterior portion of the tract differs: in place of "c," the third loop, and of the normal supra-duodenal loop, there are a set of irregular small loops. The cæca are short but wide and in the natural condition contain faecal matter. The rectum is short, wide, and straight. I am disposed to think that the type in *Aramus* is more archecentric than the types displayed by the Cranes and Rails. Although the axial loop with the diverticulum on its lower limb is characteristically Ralline, the general conformation of Meckel's tract is much more like the

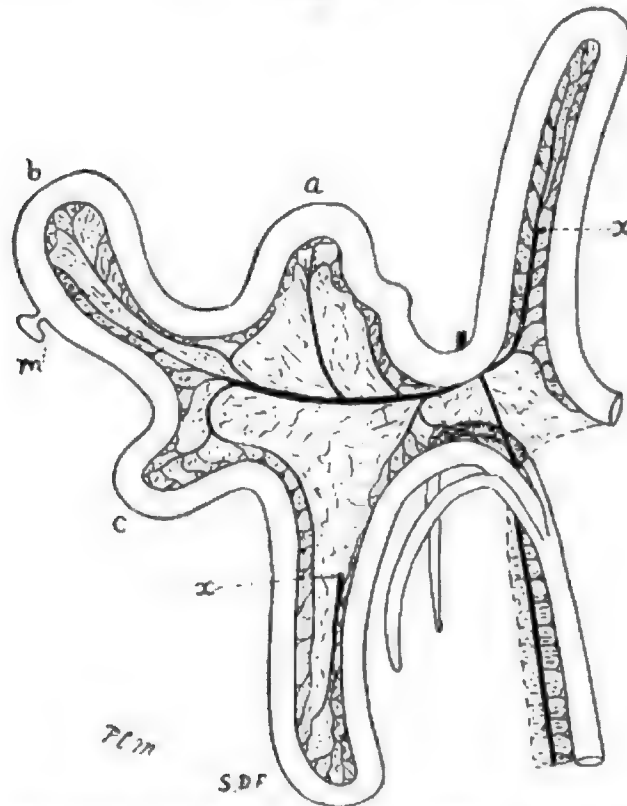
Fig. 43.

Intestinal Tract of *Aramus scolopaceus*. Lettering as in fig. 41.

archecentric condition, and this similarity is increased by the moderate length of the cæca and the absence of a specialized supra-duodenal loop. I think it is more probable that the long cæca of the Cranes and Rails are an apocentric modification than that the relatively shorter cæca of *Aramus* are pseudocentric degenerations, for, as I hope to show later, in the vast majority of cases where the cæca are obviously degenerate, the "bridging" factor or factors from the duodenal vein, which originally drained them, persist to drain a specialized supra-duodenal loop, and there is no trace of this in *Aramus*.

(3) *Psophiinae*.—As the position of *Psophia* is one concerning which there has been no little difference of opinion, it is interesting to find that the conformation of the gut in *Psophia crepitans* (fig. 44) is typically Ralline. As will be seen, it conforms in every way to the character typical of the Rallidæ. As it is probable that the differences between the type in the Cranes and that in the Rails is due merely to the larger size of the former, there is no reason to be drawn from the character of the gut for placing *Psophia* preferentially either with the Cranes or with the Rails. It displays the ground-form common to both sets. *Psophia obscura* is simplified in the direction of *Cariama* and the Bustard; the loops on either side of the axial loop, i.e. "a" and "c," have practically disappeared, so that the conformation in *Otis* is closely imitated.

Fig. 44.



Intestinal Tract of *Psophia crepitans*. Lettering as in fig. 41.

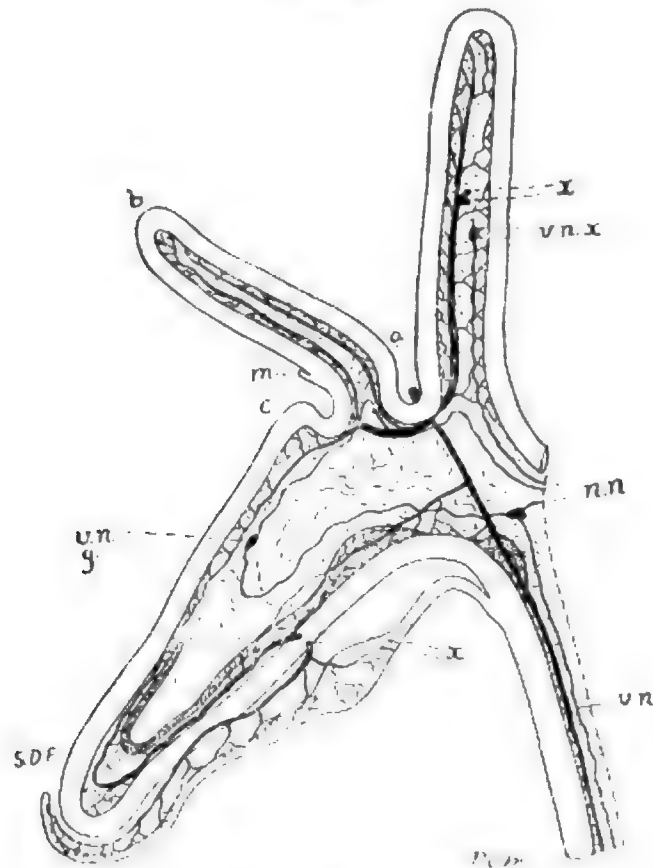
DICHOLOPHIDÆ.—I have already described and figured the intestinal tract in *Cariama cristata* (26. fig. 14), and the condition in Burmeister's *Cariama* (*Chunga Burmeisteri*) is practically identical. The duodenum is a long narrow loop. Meckel's tract displays the Ralline loops "a" and "b"; but the two are merged proximally, "b" displaying a Meckel's diverticulum on the distal limb. There is no trace of loop "c"; but there is a large supra-duodenal loop drained partly by a "bridging" vein, and having the long cæca closely applied to it. The rectum is straight but of fair length. It is plain that the intestinal tract of the Dicholophidæ presents an apocentric character of a definite nature, but which may be regarded as a simple derivative of the type shown in



the Rallidæ and Gruidæ, the loops of Meckel's tract being long and straight, the first and second being partly fused and the third having disappeared.

OTIDIDÆ.—I have had the opportunity of examining only *Otis tarda*, the Great Bustard. In it (fig. 45) the duodenum is a long narrow loop. Meckel's tract is thrown only into two loops, of which the second is a very large supra-duodenal loop drained by a pair of large bridging vessels, and has long and peculiar cæca closely applied to it. The proximal loop I take to be the axial loop seen in the Rallidæ; it bears upon it, low

Fig. 45.

Intestinal Tract of *Otis tarda*.

v.n., nerves entering mesentery; v.n.x., ganglion in duodenum from which nerves pass to cæca and supra-duodenal loop; v.n.g., large ganglion of visceral nerve; v.n., branch of visceral nerve in rectum.

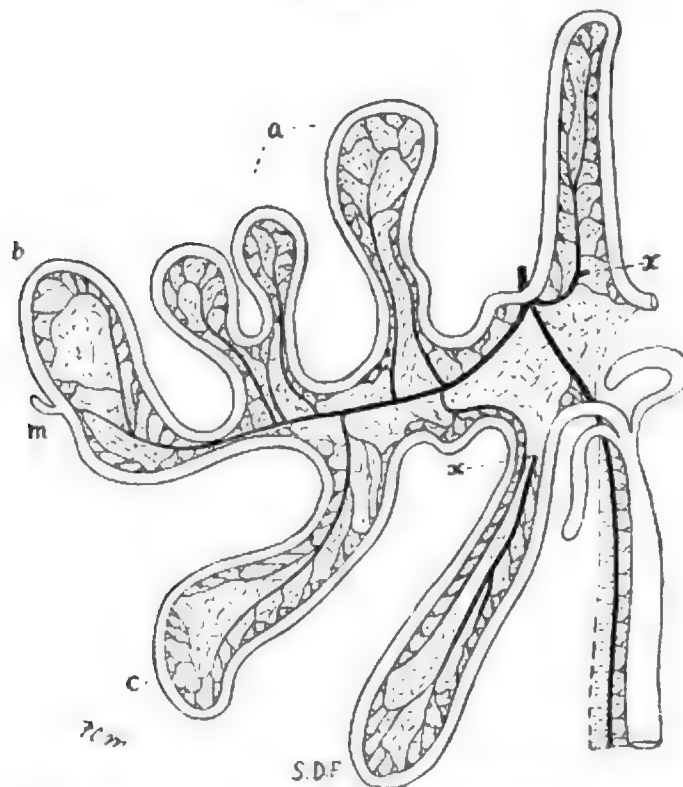
down on its distal limb, a Meckel's diverticulum. A pair of very small but quite definite folds, marked "a" and "c" in the figure, I take to represent the similarly designated large loops in the Rallidæ and Gruidæ.

The intestinal tract of *Otis* is certainly markedly apocentric. The loops are all very definite and the supra-duodenal loop in particular is highly specialized, being closely applied to the duodenum, over which it lies in the unfolded condition, and from which it receives not only a pair of bridging veins, but two branches of the autonomic visceral

nerve coming from a special ganglion in the duodenal loop (fig. 45, *v.n.x.*). The peculiar cæca which have been described by Beddard (2. p. 332) are specialized not only in their great length but in their internal structure. The general character of the gut, however, especially if I am correct in my interpretation of the small folds marked "a" and "c," is obviously Ralline. The resemblance between the guts of *Otis* and of the Tinamus is certainly striking, the only notable difference being that in the Tinamu the cæca are less specialized and that Meckel's diverticulum lies distad of the great loop of Meckel's tract rather than actually on it. I regard the closeness of the resemblance as not definitely morphological.

RHINOCHETIDÆ.—In *Rhinochetus jubatus*, the Kagu (fig. 46), the duodenum is

Fig. 46.



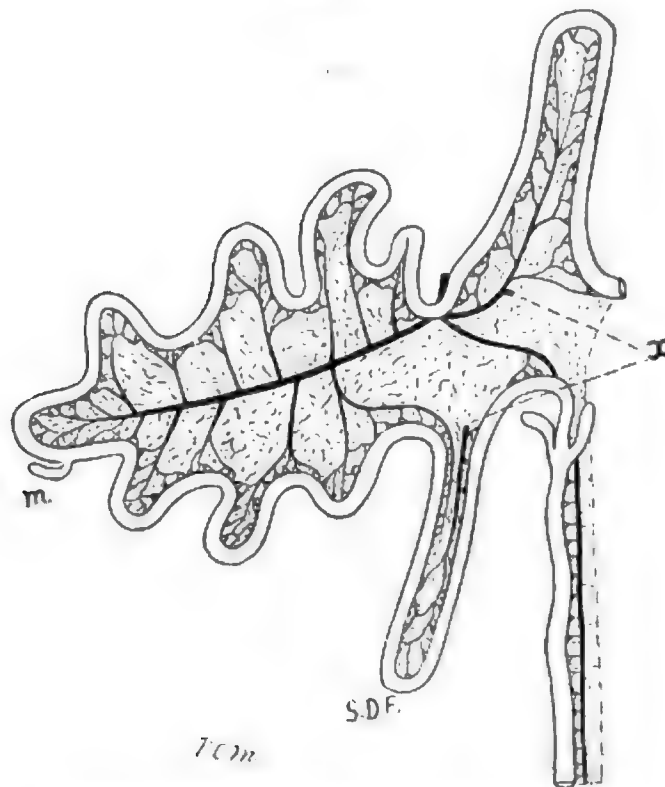
Intestinal Tract of *Rhinochetus jubatus*. Lettering as in fig. 41.

a simple, short, and narrow loop. Meckel's tract shows first a pair of minor loops, the second of which is double, then an axial loop with a large diverticulum about the middle of its distal limb, then a large simple loop marked "c," then a long narrow supra-duodenal loop with a bridging vein. The cæca are rather short, and the rectum is straight, wide, and of moderate length. The intestinal tract of this bird certainly differs considerably from that of other members of the Gruiform assemblage. The most important differences are the presence of an additional loop on Meckel's tract, the circumstance that the whole of that tract, with the exception of the supra-duodenal

loop, displays in the unfolded condition a slightly spiral twist, and the shortening of the cæca, a character shared with *Eurypyga*. The resemblance to the Balline type, however, is fairly strong. Meckel's tract is produced into a set of minor loops, of which two represent "a," while "b," with the diverticulum midway on the distal limb, and "c" are normal, and the last is a supra-duodenal loop simplified in correspondence with the reduction of the cæca. *Rhinochetus* has been compared with *Scopus*, but the character of the tract does not support this comparison. In *Rhinochetus* there is no trace of the twisted duodenum, the diverticulum is in the Gruiform position, and Meckel's tract is thrown into definite minor loops.

EURYPYGIDÆ.—*Eurypyga helias* (fig. 47) departs still more from the other Gruiformes.

Fig. 47.



Intestinal Tract of *Eurypyga helias*. Lettering as before.

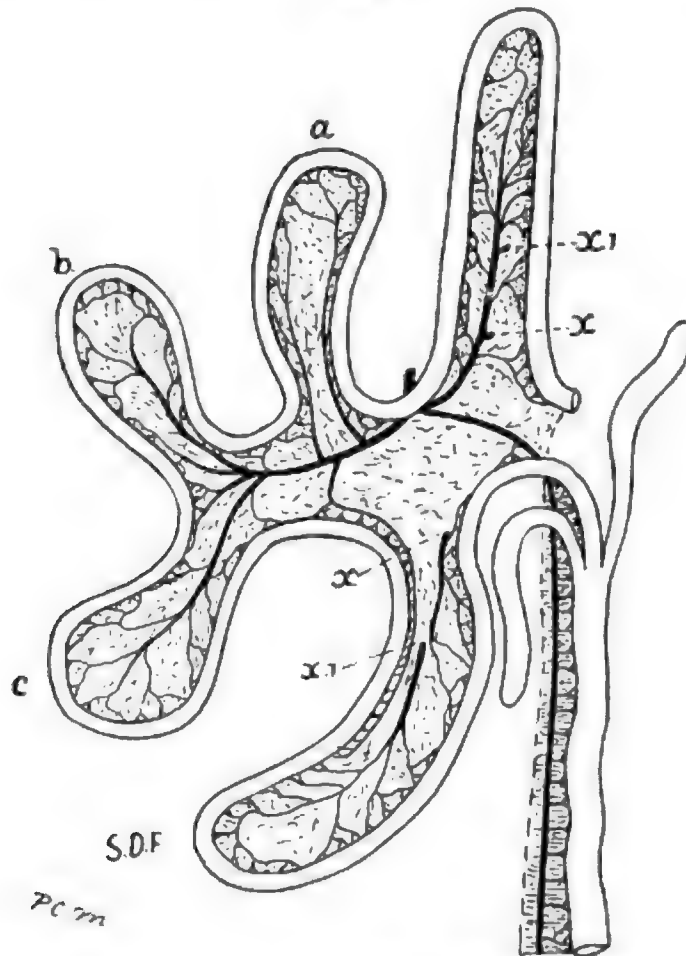
The duodenum resembles that of the other forms, but Meckel's tract is much more archcentric, the greater part of it consisting of an irregularly folded gut swung at the periphery of an oval expanse of mesentery. The large diverticulum, however, is not at the apex of the tract, but in the typical Gruiform position on the distal limb of the axial loop. The distal portion of Meckel's tract is a definite supra-duodenal loop with bridging vein. The cæca are vestigial, and the rectum is long and nearly straight.

HELIORNITHIDÆ.—In *Heliornis fulica* (fig. 48) the typical Ralline or Gruiform characters again appear. The duodenum is simple and narrow. Meckel's tract displays

the three loops "a," "b," and "c" very definitely drawn out. In *H. surinamensis*, the conformation is similar, although the loops are not so independent. In neither is there a diverticulum present. The posterior portion of Meckel's tract is a definite supra-duodenal loop drained by two "bridging" vessels. The cæca are of moderate length, and the rectum is as in the others.

It is plain that what I term a metacentral condition underlies the conformation of the alimentary tract in the Gruiform assemblage. This metacentre possesses a simple duodenum; Meckel's tract is produced into four straight loops, of which "b," the axial

Fig. 48.



Intestinal Tract of *Heliornis fulica*. Lettering as in fig. 41.

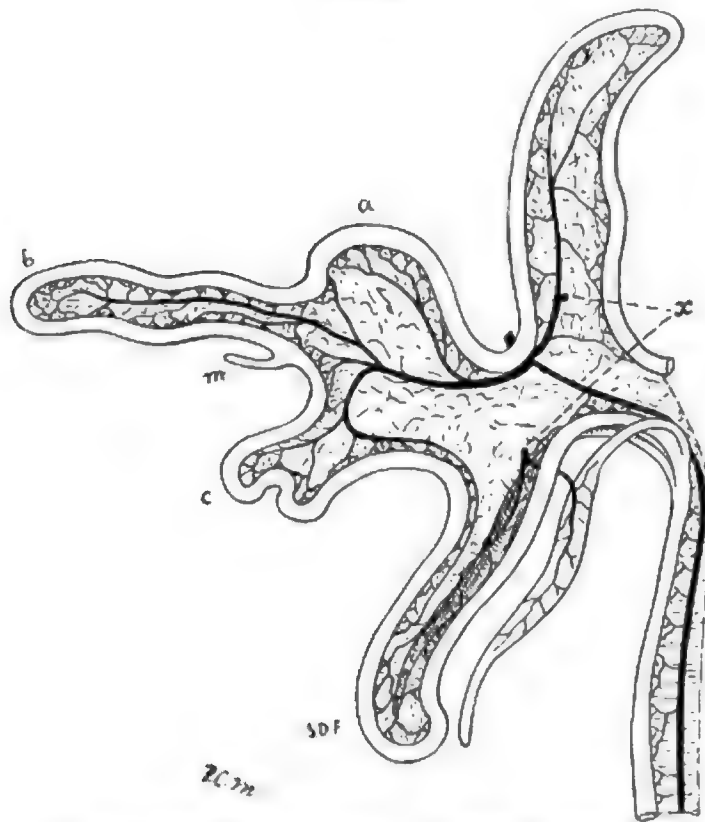
loop, carries the diverticulum on its distal limb, and of which the last is a large supra-duodenal loop drained by bridging vessels and with the long cæca closely attached to it. The Rallidæ and Gruidæ display this metacentral character without modification of any important kind. The Dicholophidæ and the Otididæ have moved apocentrically from it by reduction of loops "a" and "c" and greater specialization of the supra-duodenal loop. *Heliornis* is metacentral. *Rhinocetus* and *Eurypyga* are slightly modified, the apparent archecentricity of the latter being possibly pseudocentric.

## CHARADRIIFORMES.

## LIMICOLÆ.

CHARADRIIDÆ.—I have already described and figured the conformation of the intestinal tract in the Curlew (*Numenius arquata*, 26. fig. 15). The duodenum is straight and narrow. Meckel's tract is more archecentric than in the Gruiformes, inasmuch as the minor loops are not well separated from the general course of the gut. None the less, such minor loops exist, and markedly recall the common Gruiform type, although the condition is less apocentric. There are three main loops corresponding to "a," "b," and "c" of the Gruiform gut, and, as in that assemblage, "b" the axial loop bears on its distal limb a very large Meckel's diverticulum. The distal part of the Tract consists

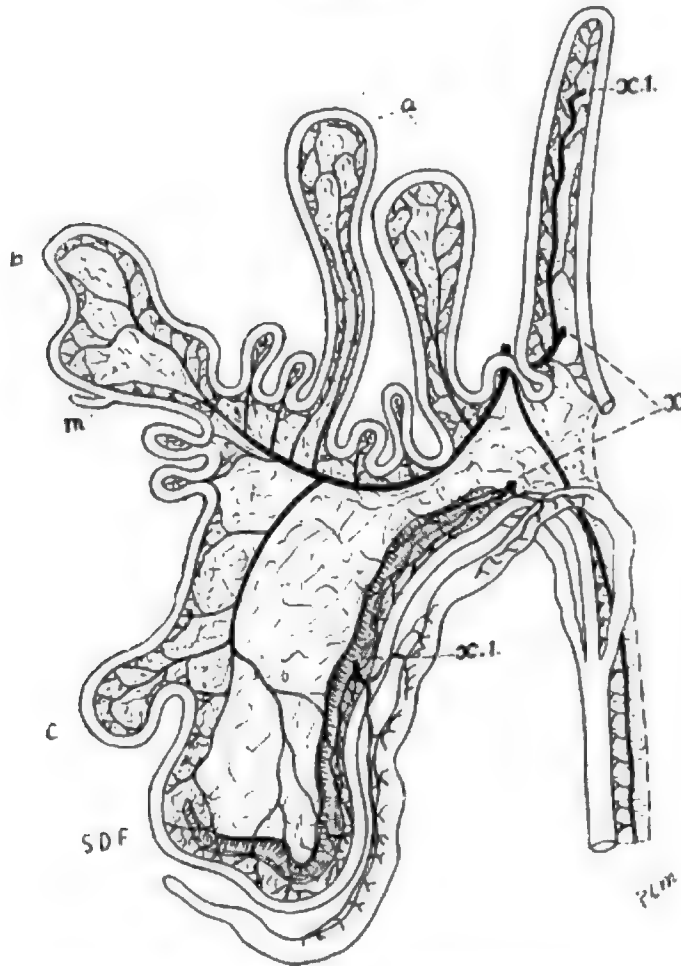
Fig. 40.

Intestinal Tract of *Tringa alpina*. Lettering as in fig. 41.

of a supra-duodenal loop not well separated from the general outline of the Tract, but drained by a "bridging" vein, and having closely attached to it the pair of long cæca. The rectum is rather short and straight. The condition in *Himantopus* is similar to this but still more archecentric—that is to say, the loops are still less marked off from the general sweep of Meckel's tract. *Vanellus vulg aris* and *V. cayennensis* are like *Numenius*. In *Tringa alpina* (fig. 49) a simple modification of the *Numenius* condition is presented. Loop "b" of Meckel's tract has grown out axially, leaving the large diverticulum at its

base, and the supra-duodenal loop is better separated. In *Recurvirostra avocetta* a still more apocentric modification in the same direction is reached. The axial loop has grown outwards to more than twice the length attained in *Tringa*, and is folded irregularly as a flat ribbon, partly rolled on itself and partly spirally twisted. The cæca remain long, and the other parts of the gut are as in *Tringa*. A still greater apocentric divergence of precisely the same kind occurs in *Scolopax rusticola* (Plate 22). I have already figured the very remarkable conformation assumed by its gut (26. fig. 16). The

Fig. 50.



Intestinal Tract of *Chionis alba*. Lettering as in fig. 41.

change is simply that the axial loop has grown still longer than in *Recurvirostra*, and the rolling-up and spiral twist is still better marked. The cæca have degenerated, and have left isolated a small supra-duodenal loop with a bridging vein.

CHIONIDÆ.—*Chionis alba* (fig. 50) shows a comparatively slight modification of the *Numenius* type, and is plainly much more archecentric than most of the Charadriidæ. Meckel's tract is relatively longer; the axial fold with its large Meckel's diverticulum is

Fig. 51.

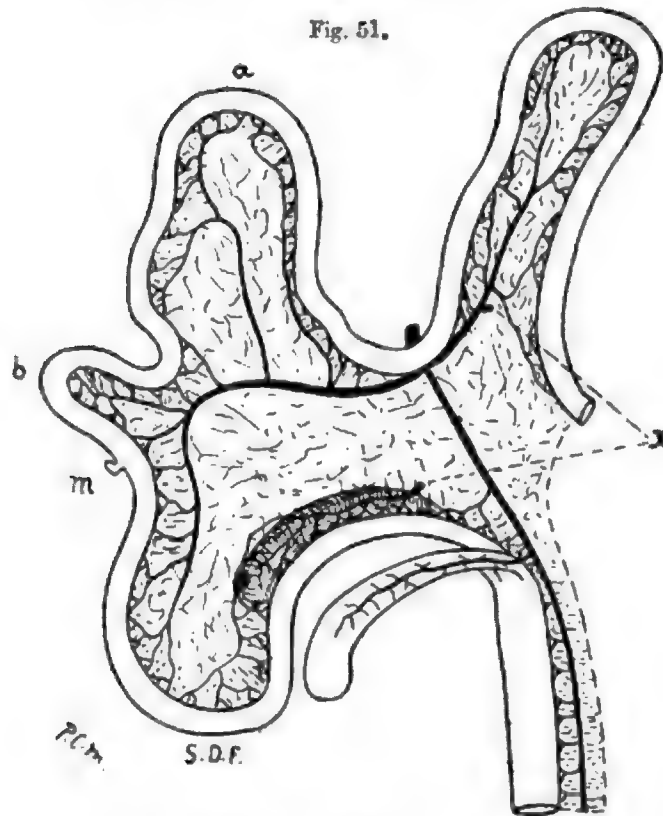
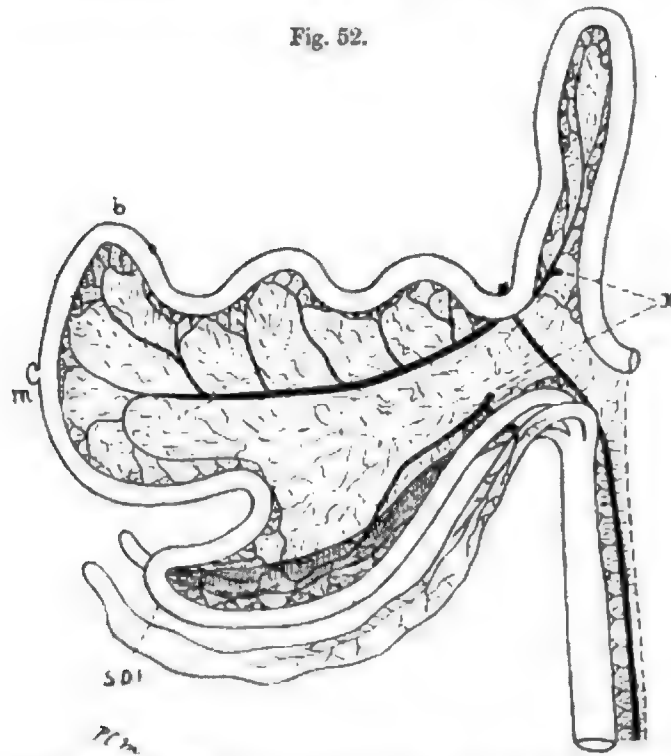
Intestinal Tract of *Glareola ocularis*. Lettering as in fig. 41.

Fig. 52.

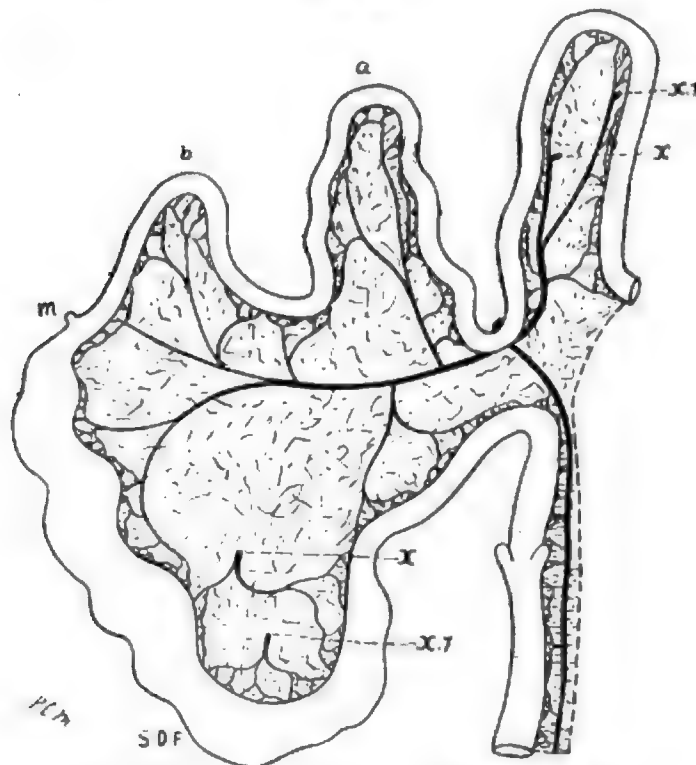
Intestinal Tract of *Thinocorys rumicivorus*. Lettering as in fig. 41.



practically identical with that of *Numenius*; but the fold "a" is represented by two loops, and loop "c" is partly fused with, or not separated from, the very large supra-duodenal loop to which the long cæca are attached.

GLAREOLIDÆ.—In *Glareola ocularis* (fig. 51), and *G. pratincola* is practically identical in this matter, another very simple modification of the *Numenius* type is displayed. The duodenum is similar; Meckel's tract is relatively shorter, and is thrown into loops "a," "b" with a small Meckel's diverticulum at its base, and a large and wide supra-duodenal loop, loop "c" not being formed. The cæca are attached in the usual way to the supra-duodenal loop, and the rectum is short, wide, and straight.

Fig. 53.



Intestinal Tract of *Parra jacana*. Lettering as in fig. 41.

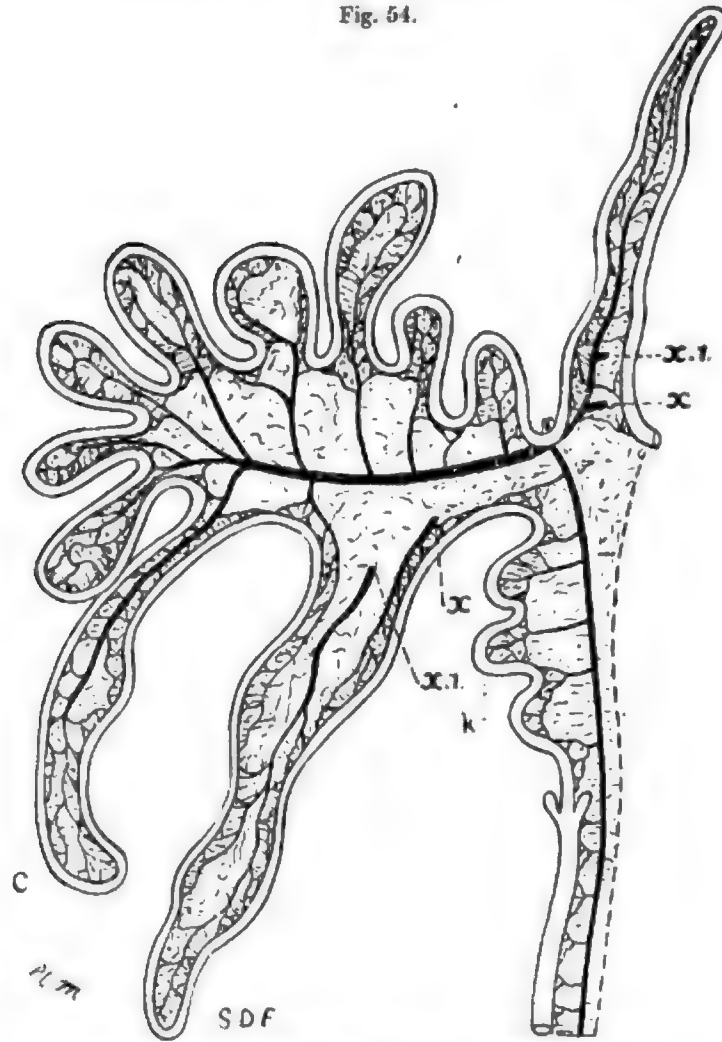
THINOCORIDÆ.—In *Thinocorys rumicivorus* (fig. 52) a condition essentially similar to that found in *Glareola* is displayed. The duodenum is similar; Meckel's tract is suspended at the end of an oval stretch of mesentery, and in it loop "b" with the diverticulum at its base is obvious, although in the drawing it is represented as turned up instead of running out in the axial line. Loops "a" and "c" are not differentiated, and the supra-duodenal loop to which the long cæca are attached is not sharply separated off except at its apex. The rectum is straight, wide, and of moderate length.

ÆDICNEMIDÆ.—In *Ædicnemus scolopax*, the Stone-Curlew, there is displayed a conformation closely similar to that found in *Thinocorys* and *Glareola*. The duodenum

is straight and simple, although rather long. Meckel's tract displays a small loop "a," then an axial loop "b" with Meckel's diverticulum on its distal limb; loop "c" is not differentiated from the supra-duodenal loop, to which the long cæca are attached. The rectum is straight. It is plain that *Edicnemus* is more archecentric than the ordinary Curlews, and that its nearest allies are the Glareolidæ, Parridæ, and Thinocoridæ.

PARRIDÆ.—In *Parra jacana* (fig. 53, p. 233) the same ground-form is obvious, although

Fig. 54.

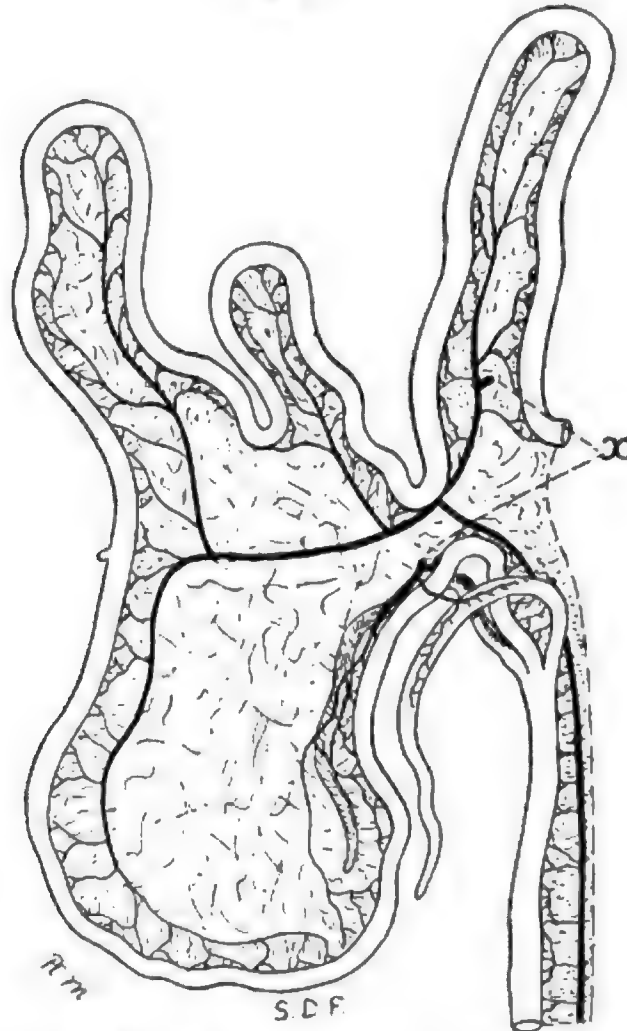


Intestinal Tract of *Pagophila eburnea*. Lettering as before.

there is a good deal of individual specialization. The duodenum is similar. Meckel's tract exhibits loops "a" and "b," the latter with the diverticulum at its base. There is no trace of loop "c," the distal portion of Meckel's tract appearing as a single very large supra-duodenal loop supplied by two "bridging" veins and with the proximal portion of the gut unusually dilated. The cæca are vestigial, and the rectum is short and straight. Except for the vestigial cæca, *Parra* is very like *Edicnemus*.

It is plain that in the Limicolæ there is displayed a ground-form very close to what I described as the Gruiform metacentre, but rather more archecentric than that. From this condition the Charadriidæ exhibit a striking set of progressively more apocentric modifications, reaching a climax in the conformation of the gut in *Scolopax*. The other

Fig. 55.



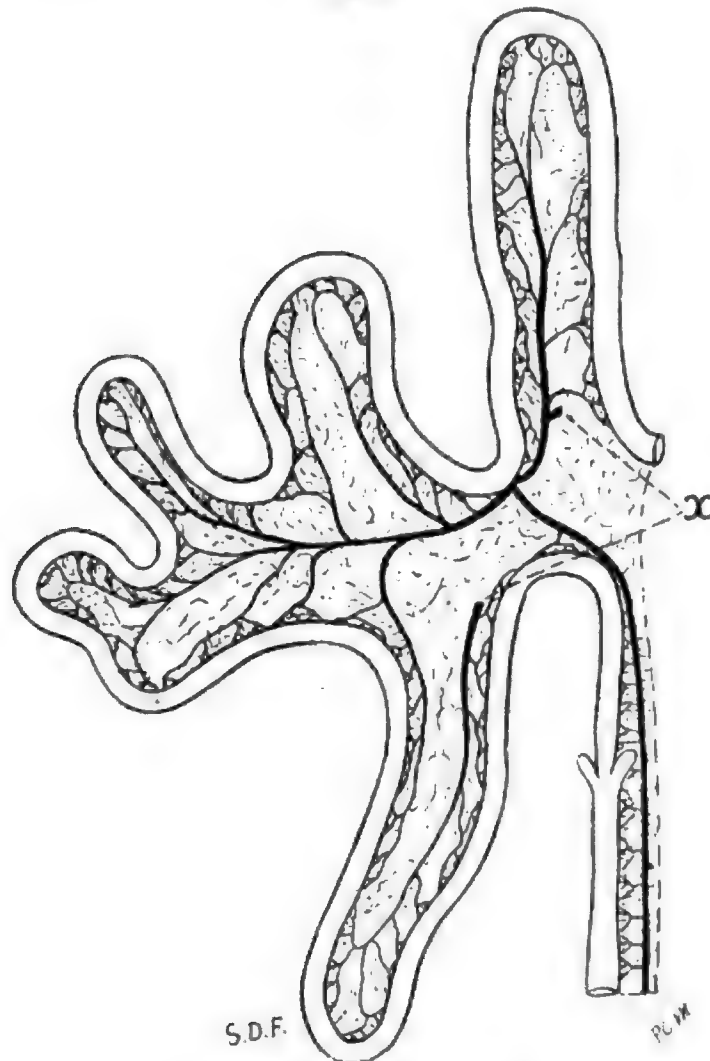
Intestinal Tract of *Stercorarius crepidatus*. Lettering as before.

families, the Chionidæ, Glareolidæ, Thinocoridæ, Œdicnemidæ, and Parridæ, all display types closely allied to that of *Numenius*, but still simpler. In other words, a form of gut like that in *Numenius* is a metacentre common to the Gruiformes and the Limicolæ: from this the Gruiformes have diverged in one direction, the specialized Charadriidæ in another, while the other families cluster about the metacentre.

## L A R I.

LARIDÆ.—I have already described and figured the conformation of the gut in *Larus marinus* (26. fig. 17). The duodenum is narrow and straight. Meckel's tract is thrown into a series of irregular loops, the first of which probably represents "a," while "b" appears as a number of closely-set short loops, proximad of the diverticulum. "c" and the large supra-duodenal loop are both present. The cæca are vestigial, and the rectum

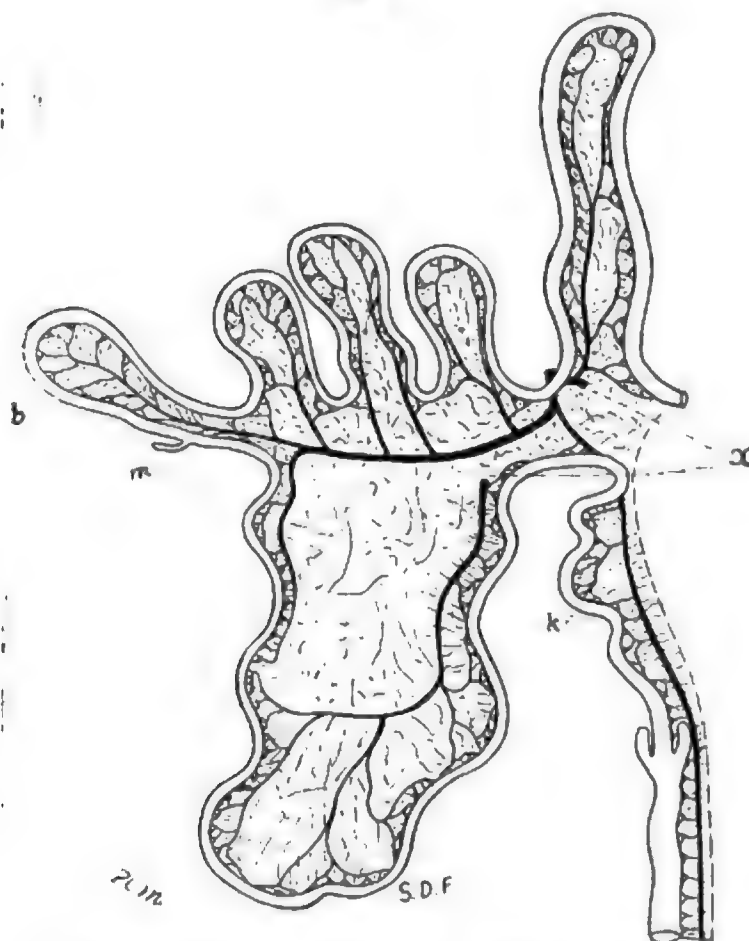
Fig. 56.

Intestinal Tract of *Sterna hirundo*.

is rather long. Other specimens of *Larus marinus* were identical, except that Meckel's diverticulum was absent, a condition frequent in the Gulls. *Larus argentatus* was closely similar, and *L. ridibundus* differed only in that the loops of Meckel's tract were more definite and were twisted into a common spiral. In *Pagophila eburnea* (fig. 54, p. 234) the general conformation is similar. Loop "c" and the supra-duodenal fold are both

larger. However, the most striking circumstance is the appearance above the cæca in the posterior part of Meckel's tract of a set of kinks drained by the rectal vein. In the drawing, the relative importance of these has been slightly exaggerated; but I was anxious to call attention to them, as their presence suggests either an unlikely affinity between the Laridæ (and the Alcidiæ) and the Pelargo-Colymbomorphine assemblage, or, more probably, that the existence of this kink is a multiradial apocentricity to which too much importance must not be attached. In *Stercorarius crepidatus* (fig. 55, p. 235) a

Fig. 57.



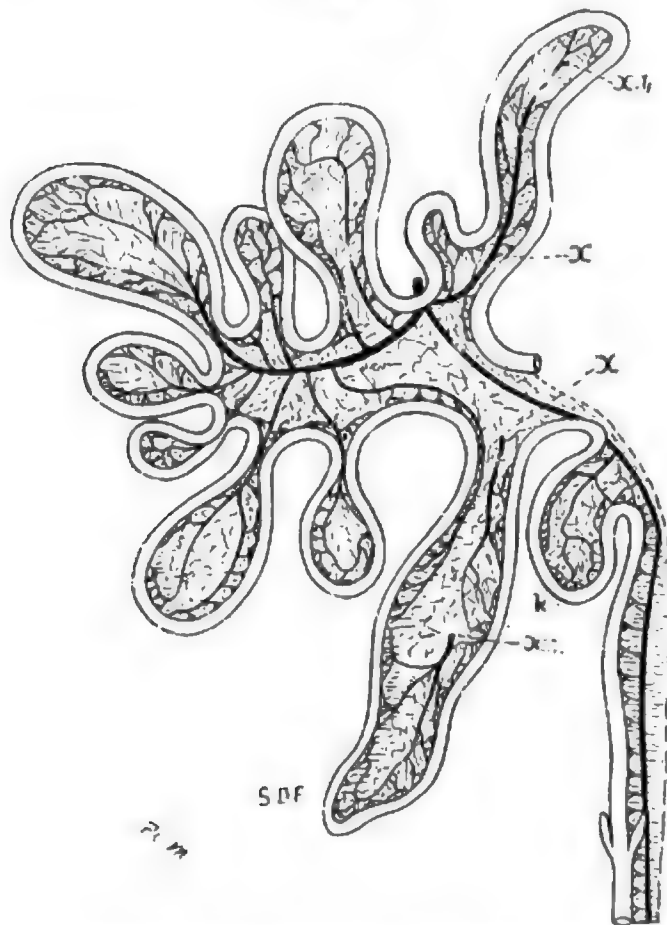
Intestinal Tract of *Pratercula arctica*. Lettering as in fig. 41.

more archecentric type of gut is displayed, the arrangement rather closely resembling that found in *Thinocorys* and *Glareola*. The duodenum is simple. Meckel's tract exhibits two loops proximad of the diverticulum, while distad of it is a very wide area representing a supra-duodenal fold and an undifferentiated loop "c." The cæca are long and the rectum is straight. In *Sterna hirundo* (fig. 56) the conformation is more apocentric, and the pattern resembles that in many of the specialized Gruiform and Charadriiform types. Meckel's tract is thrown into three minor loops, which, however, are better left

unidentified, as the diverticulum is not present, and there is a highly specialized supra-duodenal loop left free by the degeneration of the cæca and closely resembling the duodenum in shape. This similar moulding of the duodenum and the supra-duodenal loop is a condition found in many of the higher forms with relatively short guts.

**ALCIDÆ.**—In *Fratercula arctica* (fig. 57) a conformation of the same general character as that in many of the Gulls appears. The duodenum is of moderate size and not twisted. The greater part of Meckel's tract consists of a set of short loops, the axial of which bears a large diverticulum in the Ralline position, and of a very large supra-

Fig. 58.

Intestinal Tract of *Lomvia troile*. Lettering as before.

duodenal loop from which there has not been separated loop "c." Above the vestigial cæca is the curious supra-cæcal kink to which attention was drawn in certain Gulls. In *Lomvia troile* (fig. 58) a Gull-like pattern is displayed. There is no diverticulum to indicate the exact topography. There is a well-formed supra-duodenal loop and a large supra-cæcal kink. The cæca are vestigial, and the rectum is extremely short.

The Lariidæ and Alcidiæ are families of birds typically fish-eating, and in which lengthening and narrowing of the gut has to be allowed for. That allowance having

been made, the various conformations exhibited by the different genera of both families (from the point of view of conformation of the gut no distinction can be made between the families) appear obviously to belong to the simpler Ralline and Charadriiform patterns. The only other possible suggestion of affinity is provided by the existence of the supra-cæcal kinks in some Gulls and Hawks; but, as the other portions of the gut are so unlike the conformations found among the Pelargo-Colymbomorphine assemblage, I think the presence of the kinks in these few forms must be taken as a multiradial modification.

*Pteroclo-Columbine Assemblage.*

**PTEROCLES.**—I have already described and figured the gut in *Pterocles bicinctus* (26. fig. 19). The duodenum is straight and rather narrow. Meckel's tract is expanded to form three definite loops. The first of these is long, expanded at its apex, and curiously bent on itself. The second is an axial loop bearing Meckel's diverticulum at its apex. The third is a definite supra-duodenal loop, drained by a "bridging" vein and having the long cæca closely applied to it. The rectum is short and straight. In *Pterocles alchata* the condition is exactly similar, except that the cæca are relatively longer.

COLUMBÆ.

I have examined a large number of Columbidae, including the genera *Cathartes*, *Chalcophaps*, *Columba* (many species and varieties), *Columbula*, *Geopelia*, *Goura*, *Leucosarcia*, *Ocyphaps*, *Oena*, *Phaps*, *Phlogothraupis*, *Ptilopus*, *Starnæna*, *Treron*, and *Turtur*. The conformation of the gut is best understood by taking it as a simple but more apocentric derivative of the condition in *Pterocles*. The duodenum is a simple loop. Meckel's tract is thrown into the same three folds. The first is simpler than in *Pterocles*. The second or axial loop is usually very much longer, and it may be twisted into an elaborate spiral (26. fig. 19), and as in *Pterocles* bears the diverticulum, or a very small vestige of it marked by a ventral mesentery, or no vestige at all. The third loop is a definite supra-duodenal loop very closely modelled on the duodenum and drained by a "bridging" vein. The cæca are always vestigial and not infrequently are absent. Beddard (2. p. 308) mentions that in an example of *Tympanistria bicolor* only one vestige was present. I have found similar variations not infrequently in the varieties of the genus *Columba*, but apparently only as individual variations. The rectum is always very short and straight.

There is little difference in the conformation of the gut in the different genera and species. The larger forms in most cases have the length of gut relatively greatly increased, and the increase is most noticeable in the spirally twisted axial loop. In some small forms, such as *Oena*, the gut is absolutely and relatively shorter, and there is little trace of the spiral. Precisely a similar state of affairs exists among Passerines, where size is one of the chief factors in determining the length of the whole gut, and the consequent elaboration of the axial spiral. In *Ptilopus* and other fruit-eating Pigeons the whole gut is extremely reduced in length and is very wide. In such cases the relation of the pattern to that in ordinary Pigeons can only be guessed.



From the point of view of conformation of the intestinal tract, it does not appear that the Pteroclo-Columbæ stand in close relation to other Charadriiform birds. The only character in common is the tendency for Meckel's tract to be drawn out into long minor loops, and the particular apocentricity which reaches its climax in the elaborate spiral of the axial loop of Pigeons is different from that in the specialized Charadriidæ such as *Recurvirostra* and *Scolopax*, the difference being made plain by the relative positions of Meckel's diverticulum. The comparison with *Opisthocomus* seems to give a more fertile suggestion.

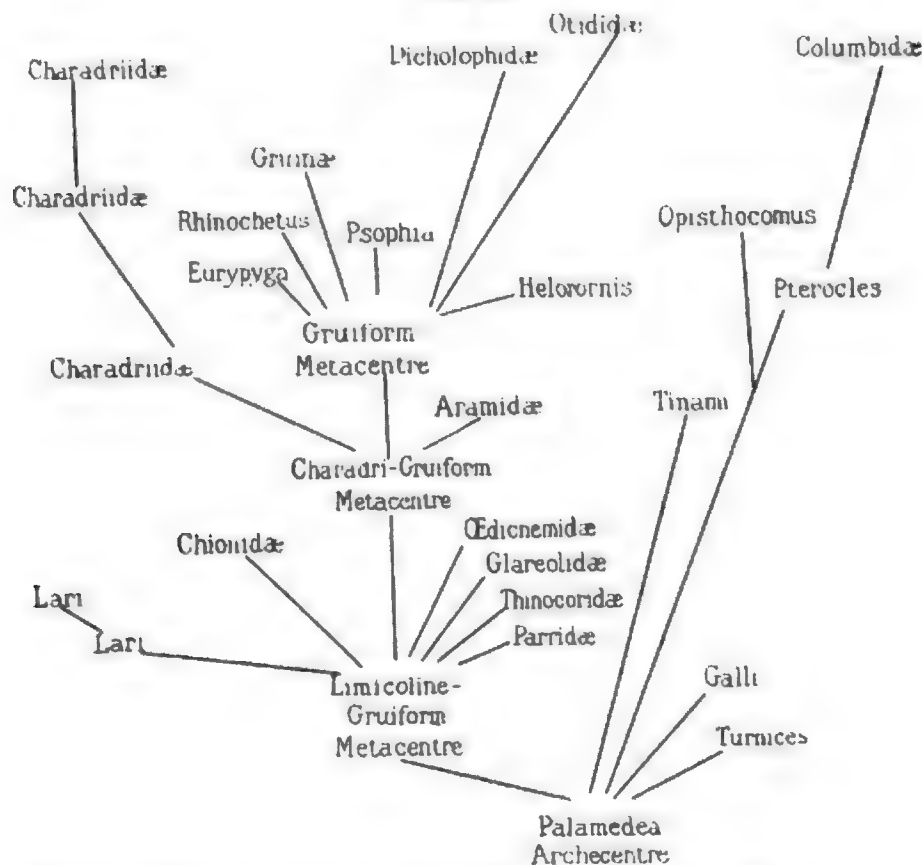
#### SUMMARY OF THE ALECTOROMORPHINE LEGION. (Plate 22.)

Gadow unites the Tinamiformes, Galliformes, Gruiformes, and Charadriiformes into the Alectoromorphæ, the first Legion of his second Brigade, and I propose now to review shortly the characters of the intestinal tract presented in this large assemblage. It must be clear that the conformations of the gut within this group do not follow many of the more generally accepted modes of subdividing the group so readily and naturally as in the case of the Pelargo-Colymbomorphine Brigade. Those, I think, who have paid most attention to the classification of birds will be prepared for this result, for the many and different divisions proposed suggest that the assemblage is still in indifferent order. From the point of view of the subject of this Memoir, it is in the first place clear that the Turnices and Galli stand apart from the other groups, inasmuch as their pattern of intestinal tract has remained markedly archcentric, differing extremely little from that in *Palamedea*. Next, the Tinamidæ retain no suggestion of Struthious affinity; they have moved far apocentrically, while the Ratites, like the Galli, have remained close to the archcentric condition. The Tinamidæ present on the one hand most striking resemblances with the Otididæ, an apocentric type of the Gruiformes. On the other hand, the radius of apocentricity on which they lie suggests that of *Opisthocomus*, *Pterocles*, and the Columbæ. *Opisthocomus*, one of the Galliformes of Gadow, certainly stands far apart from the others, and, so far as the gut is concerned, an affinity with *Pterocles* and the Columbæ is most clearly indicated. The guts of Columbæ and of *Pterocles* are extremely similar, and there is no indication of any affinity with the conformations exhibited in the other Charadriiformes or Gruiformes.

The Galli, Turnices, *Opisthocomus*, and Pteroclo-Columbæ having been disposed of, there is less difficulty in arranging the conformations of the gut in other members of the Alectoromorphine Legion in coherent order. A conformation that is a simple derivative of the archcentric form appears to underlie all of them, and this may be called a Limicoline-Gruiform metacentre. The duodenum is simple; Meckel's tract is slightly elongated, but the elongation is proximal of the diverticulum so that that appears on the distal limb of an axial loop. The distal region of Meckel's tract shows the beginning of separation into a definite supra-duodenal loop to which the long cæca are attached, and into a loop between that and the diverticulum. The rectum is short and straight. The simpler Limicoline families, such as the Chionidæ, Glareolidæ, Thinocoridæ, and Parridæ, are extremely close to this Limicoline-Gruiform metacentre; and the Lari, which from this point of view present no clear distinction into Alcidae and

Laridæ, are derivatives of the pattern only slightly modified by increased length. A modification of the Limicoline-Gruiform metacentre is found in many of the simpler Charadriidæ such as *Numenius*, and consists in the gradual shaping of Meckel's tract into three loops and a supra-duodenal loop. Of the three, one is axial and carries a large diverticulum on its distal limb. From this Charadri-Gruiform metacentre one line of progressively increasing apocentricity, consisting chiefly in a lengthening of the axial loop, is attended by degeneration of the cæca; it runs through *Tringa* and *Recurvirostra* to *Scolopax*. The Gruiform metacentre is another apocentric derivative of the Charadri-

Fig. 59.


 Evolution of the Intestinal Tract in the Alcedoromorphine Legion. (For *Helorornis* read *Heliornis*.)

Gruiform metacentre, and is reached by the first three loops of Meckel's tract, including the axial loop, being more clearly marked off and lengthening equally. Most of the Rallidæ remain in this condition. The Gruinæ are apocentric modifications of it in which all the loops, except that immediately following the axial loop, increase in length individually. The Psophiinae and Heliornithidæ are practically unmodified from it. *Rhinochetus* is modified only in that the first loop of Meckel's tract is represented by two loops, and that the cæca are reduced. *Eurypyga* is more modified, its apparent simplicity being almost certainly secondary. The Dicholophidæ and the Otididæ are very apocentric modifications of it, the apocentricity consisting chiefly in the reduction

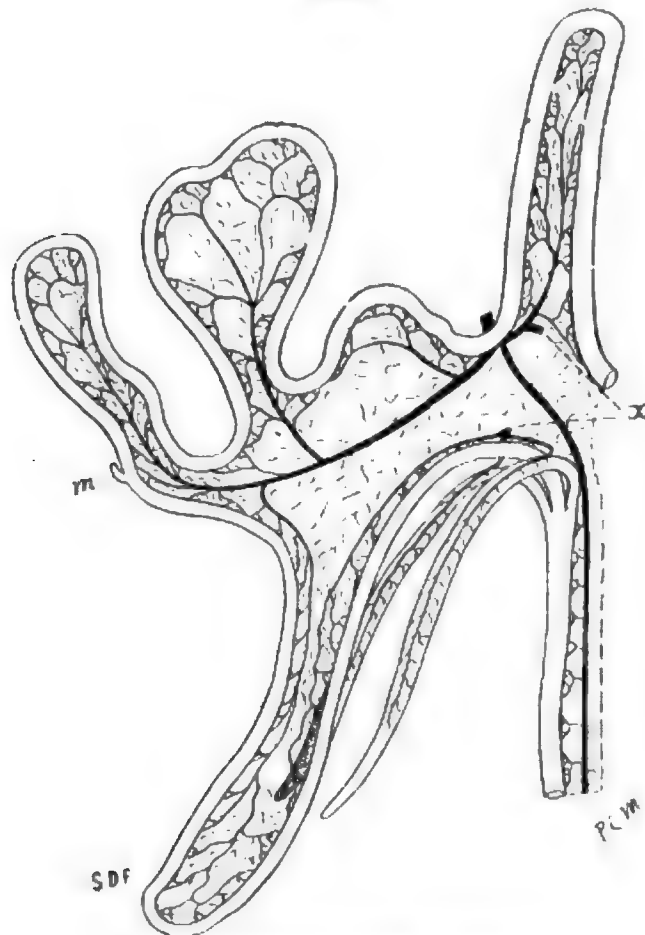
of the first and third loops of Meckel's tract and the great elongation of the axial and supra-duodenal loops. *Aramus* is more difficult to place. It appears to be certainly more archecentric than other Gruiformes, and is to be derived either from the Charadriiform-Gruiform metacentre or, even more archecentrically still, from the metacentre common to the Limicoli and Gruiformes.

## CUCULIFORMES.

### CUCULI.

CUCULIDÆ.—I have examined the intestinal tract of *Cacomantis lanceolatus*, *Carpococcyx radiatus*, *Centropus* (species?), *Crotophaga ani*, *Guira piririgua*, and *Scythrops novæ-hollandiæ*, and find that it presents the same conformation in all. The duodenum (fig. 60) is straight and narrow. Meckel's tract is not very definitely produced into

Fig. 60.



Intestinal Tract of *Carpococcyx radiatus*.

loops, but on its periphery there are two loops anterior to the diverticulum, and, posterior to it, one very long supra-duodenal loop to which the long cæca are attached. The rectum is always straight, but differs in length, being extremely short in some Cuckoos.

**MUSOPHAGIDÆ.**—I have examined several specimens of *Corythair chlorochlamys* and *C. persa*, and have already figured the intestinal tract (26. fig. 20). The whole gut is short and wide, in obvious association with frugivorous habit. This circumstance and the fact that all the specimens I have seen were affected with tubercular nodules which made the examination of the gut unsatisfactory, make it impossible to say anything very definite regarding these forms. The duodenum is straight and of moderate width. Meckel's tract appears in two portions, the proximal of which is a short, nearly circular expanse on which there was no trace of a diverticulum, and the distal a supra-duodenal loop very closely moulded on the duodenum and supplied by a large bridging vein. The rectum was short and wide, and I found no trace of cæca.

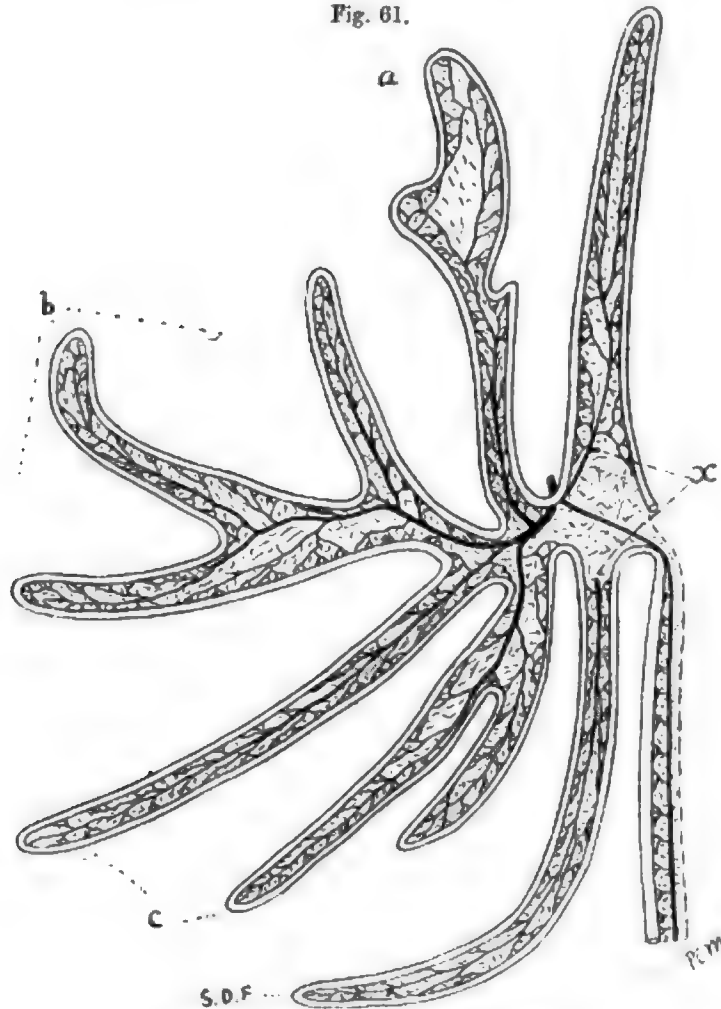
# PSITTACI.

**TRICHOGLOSSIDÆ: PSITTACIDÆ.**—Of the first family I have examined species of *Trichoglossus* and *Lorius*; of the second, species of *Ara*, *Cacatua*, *Conurus*, *Chrysotis*, *Eclectus*, *Palæornis*, *Psittacus*, and *Stringops*; but, as the conformation of the gut does not differ in any appreciable fashion according to the families and subfamilies, I shall treat them together. The larger forms have the gut relatively much longer than the smaller forms, but, under the diversity so caused, the common type is apparent. In all, the gut is very long and of small calibre; the walls are thin, and the loops are folded upon each other, and twisted and doubled in a complicated fashion. The masses of twisted gut are bound together by connective tissue usually loaded with fat, and "bridging" connections between the blood-vessels in adjoining loops are common. I have already figured (26. fig. 21) the type as displayed in *Ara ararauna*. The duodenum is long, narrow, and usually curved. Meckel's tract is drawn out into very long and narrow loops, of which the last is always a long supra-duodenal loop with a "bridging" vein. Of the others, three usually are apparent as in *Trichoglossus*, and any of these three may become compound. Thus in *Stringops* (fig. 61), of the proximal loops (marked "a" and "b" in the figure), "a" is expanded and shows traces of subdivision; "b" is subdivided into three; "c" appears as two loops, one of which is further subdivided, and only a comparison with other forms shows that the great length of the tract has brought about this complexity. I am not confident about the position of the diverticulum. In *Ara* there was present what I took to be a small representative of it at the apex of loop "b," and in one other Parrot I have noted a similarly placed trace. But in the others, including several other specimens of *Ara ararauna*, and in other species of *Ara* there was no trace. The cæca always are absent, and the straight rectum varies in length.

The diet of the Cuculidæ, consisting of insects, fruit, and flesh, is not of a nature to have caused much homoplastic modification, and the conformation of the gut is such as to make it possible to derive it from any fairly archecentric type. Garrod (13) and others have suggested an affinity between the Cuculidæ and the Galli, and, in so far as the conformation of the gut in Galli is archecentric, there is nothing definitely against such an origin of the Cuculine gut. On the other hand, there is nothing definitely in its favour, for such apcentricity as is indicated in the gut of the Galli is different from

that found among the Cuculidæ. In these, as we have seen, the tendency is for the anterior portion of Meckel's tract to be produced into two loops, and this mode of apocentricity is typical of Coraciiform birds. The reduced gut of the Musophagidæ might have come from any simple source. The Psittaci live largely on hard grains and

Fig. 61.

Intestinal Tract of *Stringops habroptilus*.

*a*, *b*, *c* and S.D.F. are the four loops of Meckel's Tract typical of the Psittaci; *a*, *b*, and *c* being here subdivided, while S.D.F. is a supra-duodenal loop.

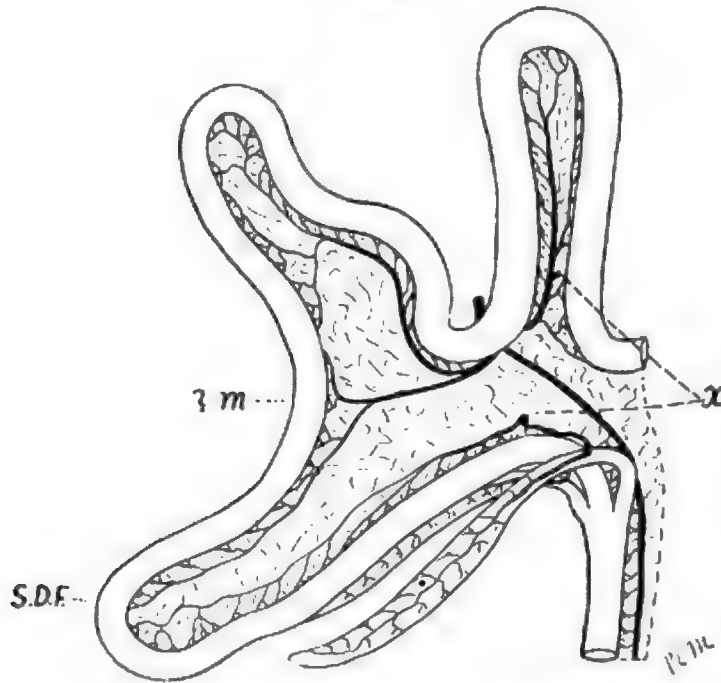
seeds, and this habit, together with the large size of many of the forms, has no doubt greatly added to the length of the gut and helped to disguise its morphological form. That conformation is markedly apocentric, as shown by the complicated folding of the loops, the length of the loops, the individuality of the supra-duodenal loop, and the absence of cæca. No doubt such a type might have been derived independently from any of the more archcentric forms, from, for instance, some of the simpler Galli, as has been suggested, but it is equally easy and perhaps more natural to derive the Psittacine type from that occurring in the simpler Coraciiform birds.

CORACIIFORMES.

CORACIÆ.

CORACIIDÆ.—I have examined the intestinal tract of *Leptosoma* (species ?) and of *Coracias garrula* (fig. 62). In both, which are practically identical, the duodenum is a

Fig. 62.



Intestinal Tract of *Coracias garrula*.

short loop relatively rather wide. Meckel's tract is thrown into two rather wide loops which are separated by the diverticulum, the latter being conspicuous in *Leptosoma*, and only faintly indicated by a trace of a ventral mesentery in *Coracias*. The distal loop is a supra-duodenal loop to which the long cæca are attached. The rectum is relatively short, wide, and straight.

MOMOTIDÆ.—I have examined *Todus viridis* and some other species of the same genus. The general conformation closely resembles that in the Coraciidæ, but the part of Meckel's tract anterior to the diverticulum is divided into loops and the cæca are shorter.

ALCEDINIDÆ.—I have examined a number of these. The smaller forms do not differ in any important respect, save the absence of the cæca, from the conformation in the Momotidæ. In the larger, such as *Dacelo* (fig. 63), the first of the two loops into which Meckel's tract is thrown is very long and is wound into a spiral form. In all the Kingfishers the cæca are absent, but there is a supra-duodenal loop more or less separated from the general sweep of Meckel's tract, and drained by a "bridging" vein. The cæca have disappeared completely, and the rectum is very wide and rather long.

Fig. 63.

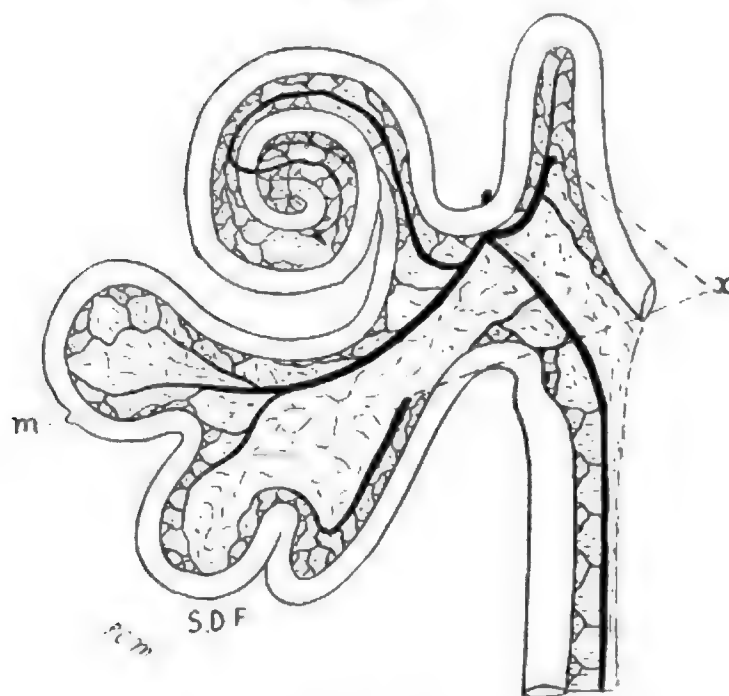
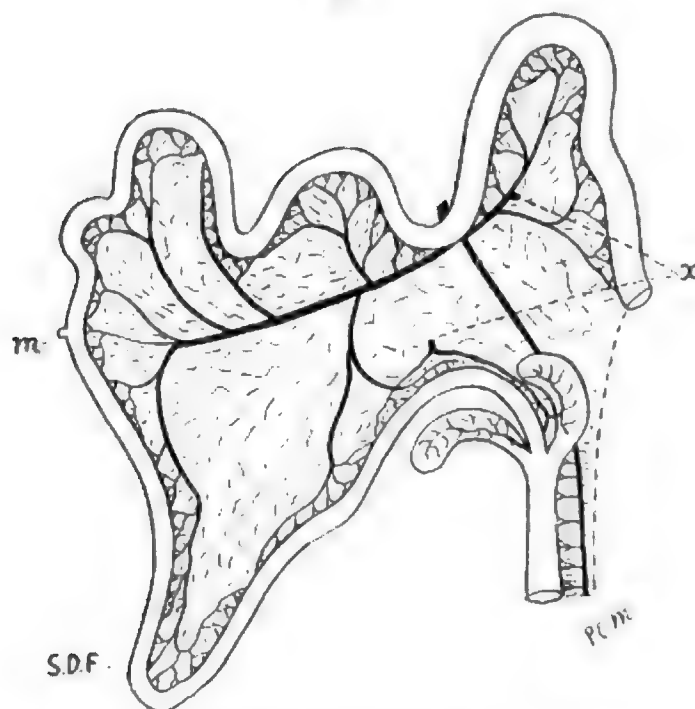
Intestinal Tract of *Dacelo gigantea*.

Fig. 64.

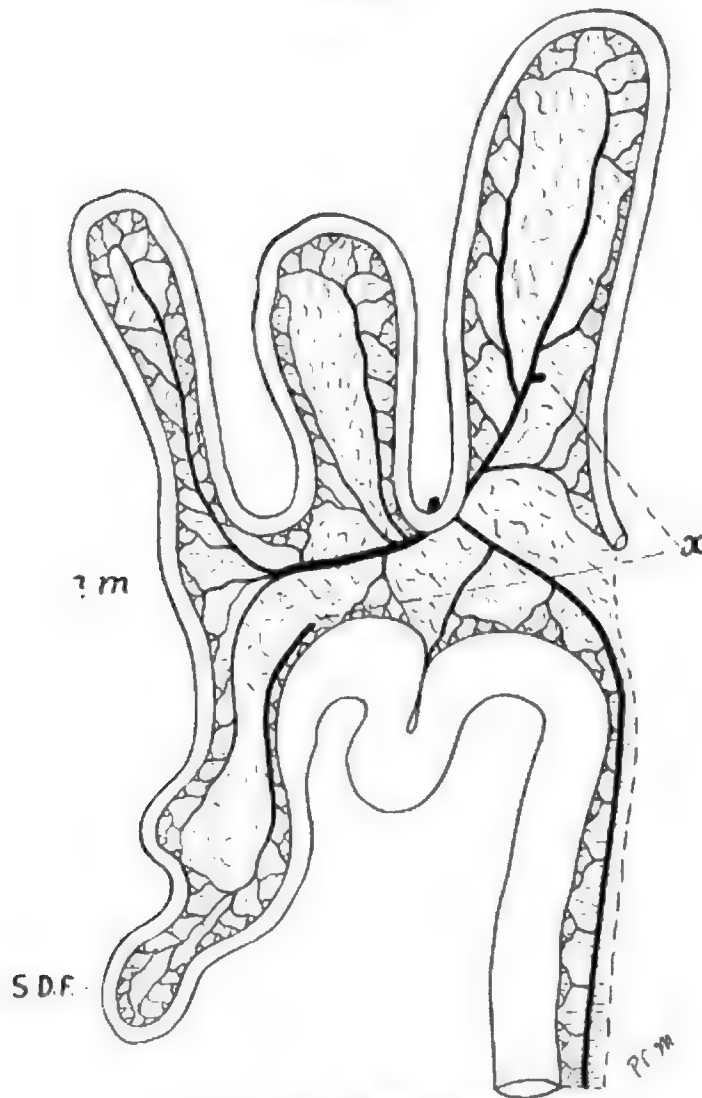
Intestinal Tract of a species of *Merops*.



**MEROPIDÆ.**—I have examined two specimens of *Merops*, the species not having been identified. In both (fig. 64) the duodenum was short and rather wide. Meckel's tract forms an expanded region, the proximal part of which showed trace of production into two minor loops, while the distal part was a long supra-duodenal loop not well separated from the general sweep of the Tract. The cæca were not long, but were wide and contained faecal matter. The rectum was short and wide. In the middle of Meckel's tract there occurred a distinct diverticulum.

**UPUPIDÆ.**—In *Upupa epops* (fig. 65) the duodenum, as in many Coraciiform birds,

Fig. 65.



Intestinal Tract of *Upupa epops*.  
? m, probable position of Meckel's diverticulum.

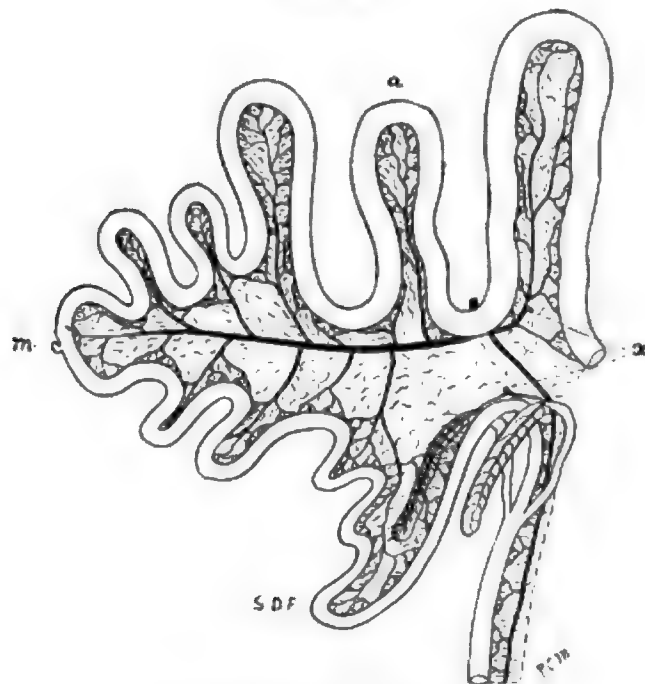
was a wide loop. Meckel's tract displayed two distinct wide loops on its proximal portion, while the distal formed a long supra-duodenal loop drained by a bridging vein. There

were no cæca, and the rectum was long, wide, and partly convoluted. In *Rhytidoceros plicatus* (26. fig. 23), and other Hornbills resemble it, the duodenum is extremely wide. Meckel's tract is thrown into three distinct long loops, of which the last is a well-formed supra-duodenal loop with "bridging" vein. The two anterior loops possibly correspond to the two loops of *Dacelo* and other *Coraci*; but the second, which is much the longer, bears a distinct diverticulum near the apex on its distal limb. There are no cæca, and the rectum is rather wide and straight. It is clear that the character of the gut does not unite the Hoopoes and Hornbills closely.

#### STRIGES.

(1) STRIGINÆ.—Of these I have examined only *Strix flammea*. The conformation of the intestinal tract in this is remarkably archeocentric (fig. 66). The duodenum is a large

Fig. 66.



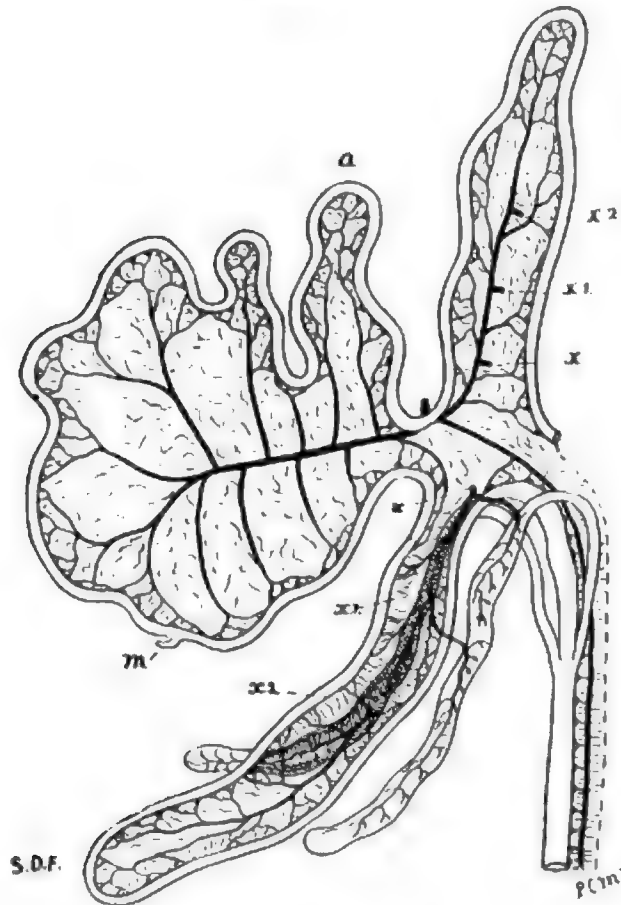
Intestinal Tract of *Strix flammea*.

but simple loop. Meckel's tract is fairly symmetrical about the middle mesenteric vein which runs out towards a diverticulum. It is produced into first one definite loop (marked "a" in the figure), and then has a circular expanse with a rather narrow neck, uniting it above to loop "a," and distally to a definite supra-duodenal loop. This expanse is partly produced into indefinite minor loops. There are two long cæca attached to the supra-duodenal loop, and the rectum is straight and of moderate length.

(2) BUBONINÆ.—Of these I have examined species of *Bubo*, *Asio*, *Athene*, *Syrnium*, *Speotyto*, and *Gymnoglaux*. Of these *Bubo maximus*, which I have already figured (26. fig. 22), *Asio*, and *Speotyto* do not differ in any important respect from *Strix*; the

supra-duodenal loop possibly is rather better separated from the general sweep of Meckel's tract. In the others, except *Gymnoglaux*, a slightly more apocentric modification has taken place. In *Syrnium aluco*, for instance (fig. 67), the duodenum is as in the others. Loop "a" of Meckel's tract is as in *Strix*, but the region between this and the diverticulum is much enlarged, so that the diverticulum is no longer at the apex of the circular expansion. The supra-duodenal loop has increased very much in size, and is well separated

Fig. 67.



Intestinal Tract of *Syrnium aluco*.

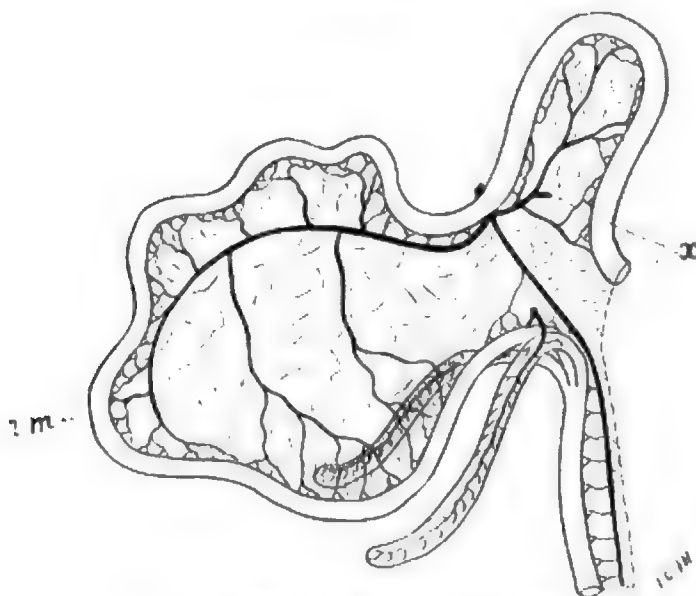
from Meckel's tract, and drained by a series of "bridging" veins. In *Bubo maculosus* and *B. poensis* the conditions are very similar to that in *Syrnium*, but the part of Meckel's tract anterior to the diverticulum appears in two well-marked loops, a conformation which recalls that in many of the Coraciæ. In *Gymnoglaux*, possibly in association with its small size, a simplification of the gut has taken place, with the result that there exists conformation closely resembling that in many of the Rollers and other simple short-gutted Coraciiform birds. Meckel's tract is thrown into two wide loops separated by the diverticulum, the posterior loop being a wide supra-duodenal loop with bridging veins.

## CAPRIMULGI.

STEATORNITHIDÆ.—I have examined only a spirit-specimen of *Steatornis*, and that in a fragmentary condition after it had already passed through the hands of other anatomists. It was easy, however, to recognize the general conformation of the gut and its resemblance to the form in other Coraciiform birds. The duodenum was short and rather wide. Meckel's tract showed two loops anterior to the diverticulum and two, not so well separated, distad of it, the second being a distinct supra-duodenal loop with the functional cæca attached to it. The rectum was long and straight.

PODARGIDÆ and CAPRIMULGIDÆ.—I have examined a number of these, several of which, however, were not identified as to species. In all, the form of the gut was essentially similar. The duodenum (*Nyctidromus albicollis*, fig. 68) is short and wide.

Fig. 68.

Intestinal Tract of *Nyctidromus albicollis*.

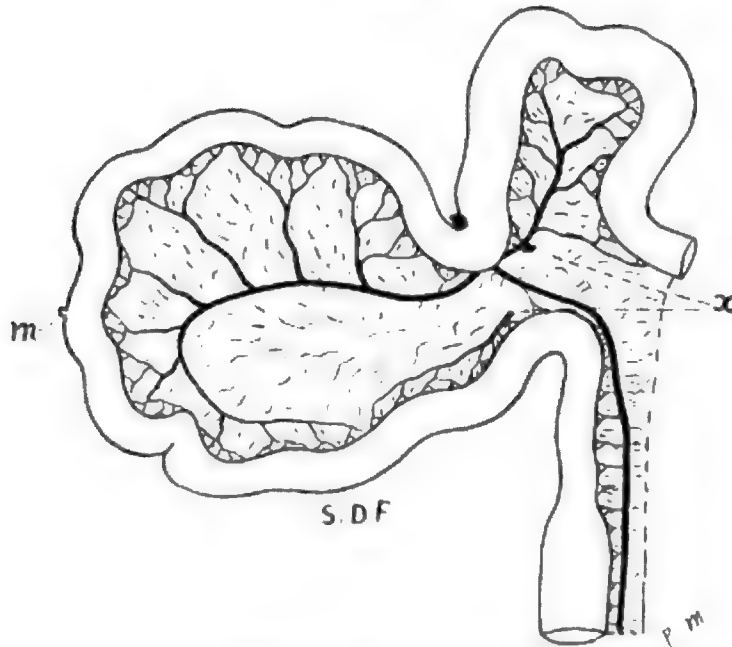
Meckel's tract, which is relatively short, appears as a circular expanse, upon the middle of which the diverticulum was present in most cases, but in some it was absent. The part of the Tract proximad of the diverticulum showed traces of expansion into the two loops so common in Coraciiform birds. The part posterior to it had the long cæca closely applied to it, and these were drained partly by a bridging vein. The rectum was relatively long and straight. This conformation found in the Caprimulgidæ is obviously remarkably archcentric, and is at once comparable with the primitive type.

## CYPSELIDÆ.

CYPSELIDÆ.—I have examined several species of Swifts, and in all found the conformation similar to that in *Cypselus apus* (fig. 69). The duodenum is short and very wide.

Meckel's tract is short, and forms a circular expanse with the diverticulum nearly at the central point. The posterior region of the tract, however, shows traces of former

Fig. 69.



Intestinal Tract of *Cypselus apus*.

complexity, in that it is drained partly by a bridging vein, a circumstance to which I attach importance as evidence that the apparent simplicity of the gut is pseudocentric. The cæca are absent, and the rectum is straight and wide.

TROCHILIDÆ.—I have examined a number of Humming-birds, and found that the conformation of the gut was in every case practically identical with that in *Cypselus*. It is worth while pointing out that the Humming-birds differ clearly in the conformation of the gut from the Passerine Nectariniidæ, although in both the small size has brought about a remarkable simplicity. The Nectariniidæ possess the Passerine nipple-like cæca, and show clear indications of the spiral twist in Meckel's tract which is a striking Passerine character, and there is no trace of either of these peculiarities in the Humming-birds.

#### COLIÆ.

I have already described and figured the intestinal tract of *Colius capensis* (26. fig. 21). It is relatively shorter and wider than in any other bird that I have examined, and this modification, no doubt due to small size and frugivorous habit, has obliterated practically completely the underlying morphological form. The gut consists of a very wide duodenum, a Meckel's tract bearing a small diverticulum, and consisting of a simple loop similar to the duodenum in size and appearance, and a short, wide rectum. There are no traces of cæca.

## TROGONES.

In *Trogon puella* (fig. 70) the duodenum is a large loop expanded towards its apex, Meckel's tract shows two loops anterior to the position where I infer the yolk-sac to have been, although there was no diverticulum left as a vestige of it. The distal portion of the Tract has the long cæca adherent to it, and these are drained by a "bridging" vein. The rectum is short and straight.

## PICI.

GALBULIDÆ.—I have not seen any of this family.

CAPITONIDÆ.—I have examined *Tetragonops Frantzii* and *Megalæma asiatica*. In these the conformation of the gut is much alike. The duodenum (fig. 71) is a short, wide loop. Meckel's tract exhibits two short loops anterior to the diverticulum, and, distad of that, forms a distinct supra-duodenal loop with "bridging" vein. There is no trace of cæca, and the rectum is straight and wide.

LYNGIDÆ.—In *Iynx torquilla* the conformation of the gut is practically identical with that in *Megalæma*.

RHAMPHASTIDÆ.—I have examined *Andigena Bailloni*, *Pteroglossus Wiedi*, *Rhamphastos ariel*, and *R. vitellinus*. In all the duodenum is very wide, and Meckel's tract and the short rectum do not differ from the form found in *Megalæma*.

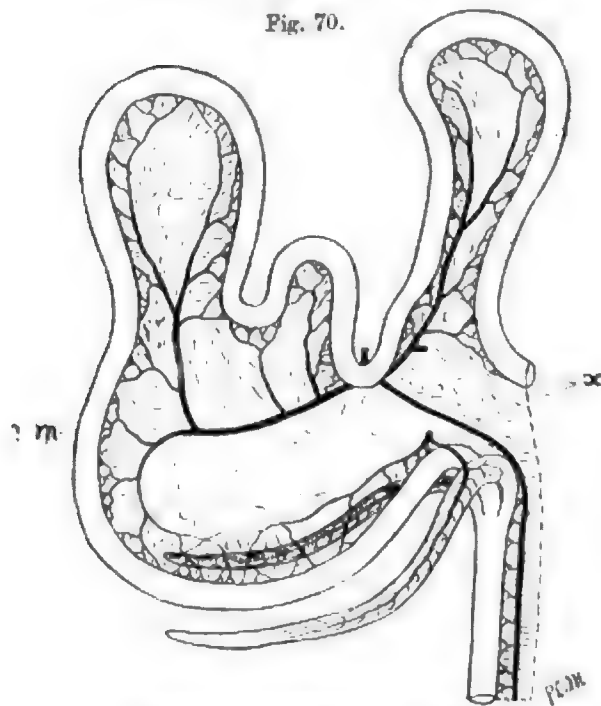
PICIDÆ.—In *Dendrocopus major*, *Gecinus viridis*, and *Leuconerpes candidus* the conformation of the gut is in every important respect similar to that found in *Megalæma*.

The Coraciiform birds tend generally towards the production of an extremely short, wide, and simple gut. The small size and the frugivorous habit, so common among them, are agencies that have combined in producing this pseudocentric simplicity. Certain forms, such as *Nyctidromus*, are readily comparable with the archecentric type, and present a simple duodenum, a Meckel's tract which is a circular expanse divided by the diverticulum into an anterior portion and a distal portion to which the long cæca are attached, and finally a straight, rather wide rectum. The changes from such a condition depend, first, on a widening of the duodenum; second, on a tendency for the portion of Meckel's tract proximad of the diverticulum to appear in two loops; and, third, for a supra-duodenal loop to become distinct in the distal portion of Meckel's tract. From this condition, various more apocentric modifications of the conformation are produced, chiefly by shortening and simplification of the tract and by reduction of the cæca.

## PASSERIFORMES.

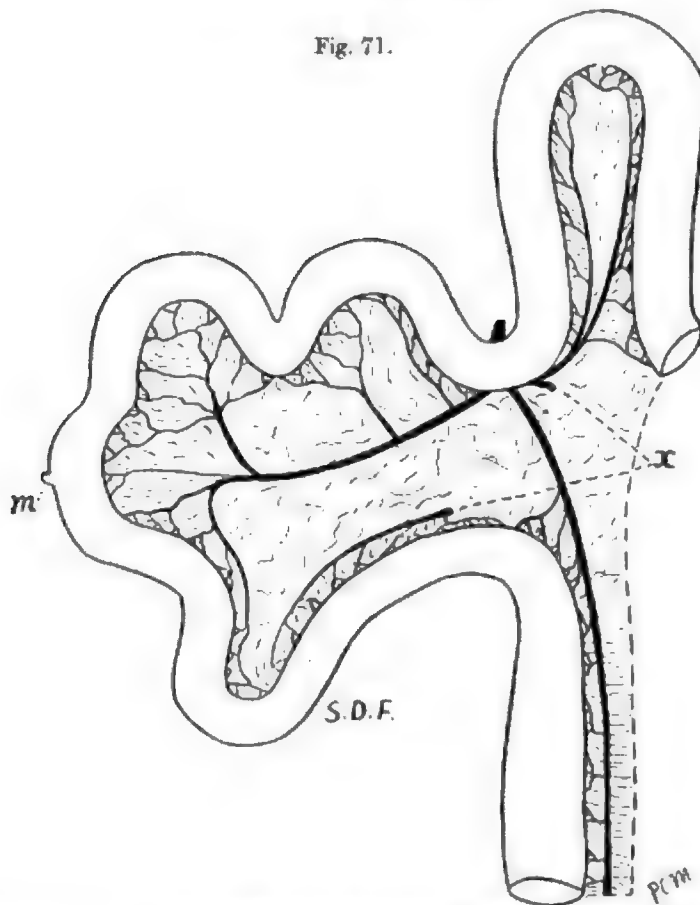
I have examined a very large number of Passeres, belonging to the family Eurylæmidæ of the Subclamatores; to the families Tyrannidæ, Pittidæ, Pteroptochidæ, Dendrocolaptidæ, Cotingidæ, Formicariidæ, and Pipridæ of the Clamatores; of the Suboscines I have examined *Menura*, and of the Oscines members of the families Alaudidæ, Timeliidæ, Pycnonotidæ, Muscicapidæ, Turdidæ, Troglodytidæ, Hirundinidæ, Campephagidæ,

Fig. 70.



Intestinal Tract of *Trogon puella*.

Fig. 71.

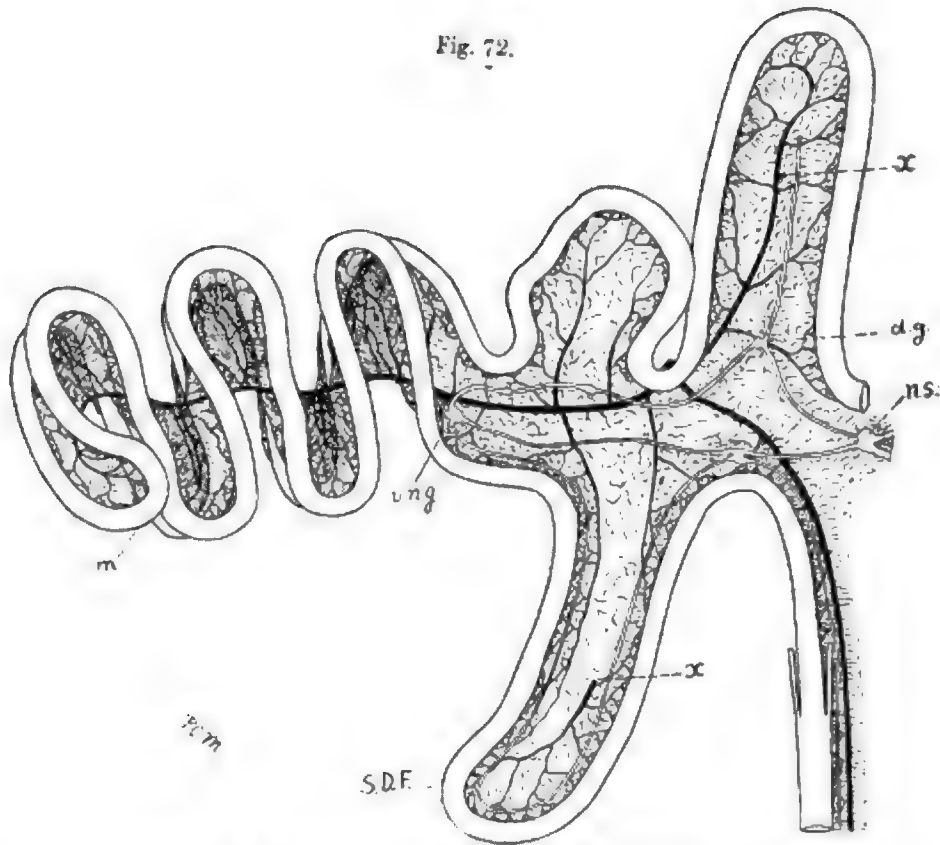


Intestinal Tract of *Megalopta asiatica*.



Dicruridæ, Ampelidæ, Artamidæ, Laniidæ, Vireonidæ, Sittidæ, Oriolidæ, Paradiseidæ, Corvidæ, Sturnidæ, Meliphagidæ, Zosteropidæ, Nectariniidæ, Dicaeidae, Cœrebidæ, Mniotiltidæ, Icteridæ, and Fringillidæ. This considerable labour from one point of view had a negative result, for I failed to find in the characters of the alimentary canal any indication of the families and groups into which systematists have subdivided the Passerines. The differences that exist among them traverse the group irrespectively of the divisions of systematists. These differences depend almost entirely on the size and habits of the birds. The larger forms have a longer gut absolutely and relatively; the fruit-eaters have the gut extremely short and wide; grain- and seed-eaters have the gut rather longer. But for these differences the conformation is remarkably similar throughout the group. The duodenum in all is a simple loop, but usually rather wide. The rectum is always short, and the cæca, although present in every case that I have examined, are reduced to short rather nipple-like structures of varying shape, but always with thick walls and only a very small central cavity. Meckel's tract presents the greatest divergences. The diverticulum is missing in the vast majority of cases. As an exception, it is extremely large in *Menura*, and in a few cases it is present. Relying partly on my own observations and partly on the extended labours of Gadow (12), I do not doubt that the diverticulum in Passeres is situated on the apical point of the large portion of Meckel's tract extending from the duodenum to the beginning of the supra-duodenal loop. In birds with a long intestinal tract, as for instance in *Corvus capellanus* (fig. 72), this portion of Meckel's tract is rolled up into a tight spiral which in the figure is represented as partly drawn out. In birds with a shorter tract, as for instance in *Cyclorhis albiventris* (fig. 73), and this may be taken as typical of the vast majority of Passeres, the spiral is represented by two distinct loops, which, in the unfolded condition, are applied very closely to one another, and the folded pair of loops have a slight spiral twist. In all Passeres there is a supra-duodenal loop very distinctly separated from the rest of Meckel's tract, modelled in the most exact fashion on the duodenum, and drained by one or more bridging veins from the duodenal vein. The conformation of the gut in the majority of Passeres, although from its short form it falls into a very simple pattern, appears in reality to be a highly specialized type, the apparent simplicity being pseudocentric. In many birds with short guts the intestinal tract is folded in an irregular and almost capricious manner, and the separate portions bear no exact relation to one another. In the Passeres the first two loops of Meckel's tract are most closely applied and extremely similar in calibre and shape, and their arrangement suggests most strongly that they have been derived by reduction from the proximal portion of what was originally a long spiral. It would appear to be certain that the small Passeres have descended from larger birds. In the same fashion, the supra-duodenal loop is so exactly modelled on the duodenum to which it is applied, as to suggest specialization rather than simplicity. In Passeres generally, the blood-vessels, instead of passing through the centre of the mesenteric expanse, run extremely closely to the intestinal coils, and contribute to the general impression given by the conformation of the gut as a highly specialized type.

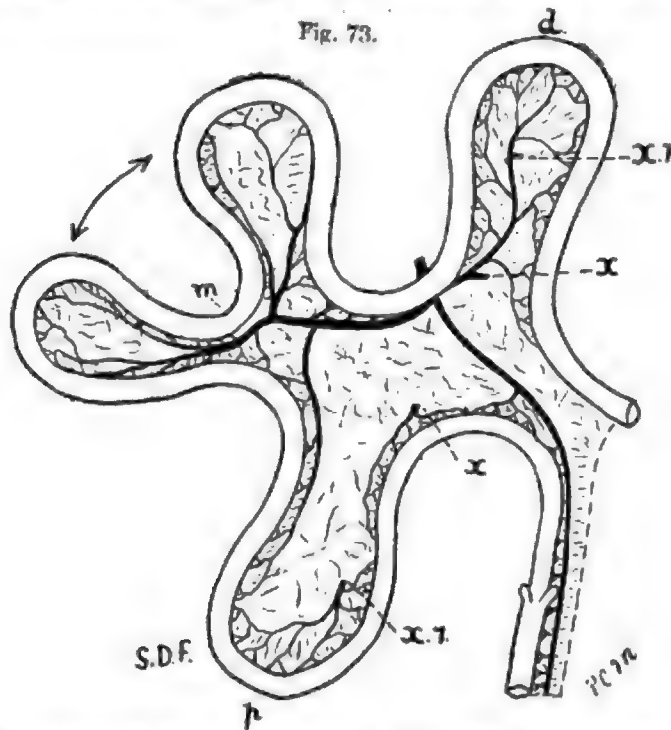
Fig. 72.



Intestinal Tract of *Corvus capellanus*; type of long-gutted Passerine.

*x*, bridging factor of duodenal vein from S.D.F. the supra-duodenal loop; *m*, position of Meckel's diverticulum at the apex of the spiral; *n.s.*, *d.g.*, *v.n.g.*, ganglia of the autonomic nerve-chain.

Fig. 73.



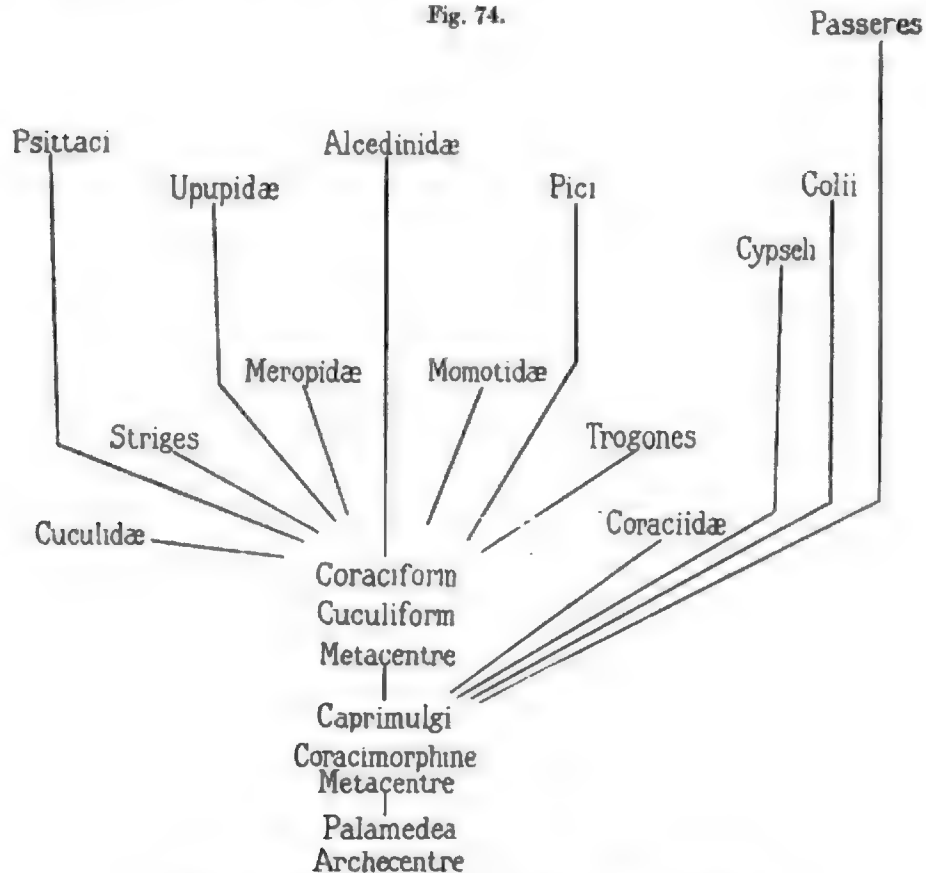
Intestinal Tract of *Cylorhis albiventris*; type of short-gutted Passerine.

*d*, apex of duodenum, which in the unfolded condition is applied to *p*, the apex of the supra-duodenal loop; *m*, position of Meckel's diverticulum, corresponding to apex of spiral in fig. 72.

## SUMMARY OF THE CORACIOMORPHINE LEGION. (Plate 23.)

Gadow (12) unites the Cuculiformes, Coraciiformes, and Passeriformes into the Coraciomorphæ, the second legion of his second Brigade. The simplest and apparently most arche-centric type of intestinal tract to be found among these birds occurs in the Caprimulgi. This, which I call the Coraciomorphine metacentre, is a simple derivative of the arche-centric type, and is changed from that practically only in the shortness and straightness of the rectum, although the duodenum tends to be rather wider relatively. From this metacentre the Passerine gut is a very apocentric derivative, the changes

Fig. 74.



Evolution of the Intestinal Tract of the Coraciomorphine Legion.  
(For Coraciomorphine read Coraciomorphine.)

being the specialization of Meckel's tract into a proximal portion which bears the diverticulum, and which is wound into a long or short spiral, and a distal portion which is an extremely specialized supra-duodenal loop. The cæca have also been reduced in size. The conformation of the Cypseli and Colii may also be an apocentric derivative of the Caprimulgid form, the apocentricity in both consisting of an immense reduction in the length of the whole gut, with degeneration of the cæca so that no vestige of them is left, and with obliteration of the loops in Meckel's tract; there may or may not be a supra-duodenal loop. The Coraciidæ present a less apocentric modifi-

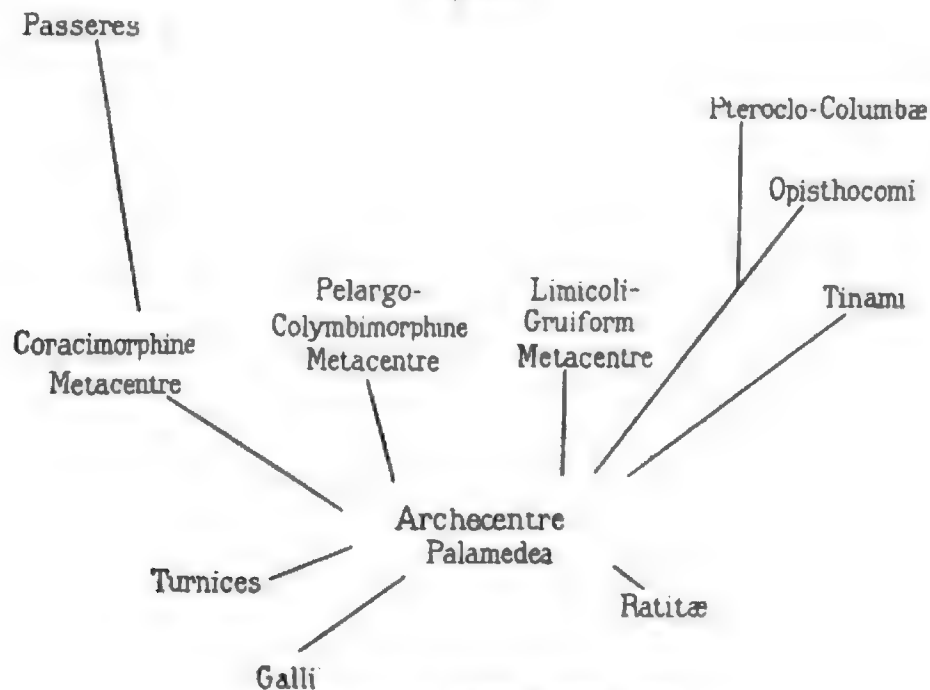
cation. Meckel's tract appears in two loops separated by the diverticulum, the posterior loop having attached to it the long cæca and so forming an incipient supra-duodenal loop. Underlying the conformations in the other types there is a central pattern which I call the Coraciform-Cuculiform metacentre, and in which the duodenum is frequently but not invariably wide; Meckel's tract is produced into two loops anterior to the diverticulum, and a single, rather wide supra-duodenal loop to which the long cæca are attached. The Cuculidæ retain this metacentral form, only slightly altered by increase of length, due no doubt to the relatively large size of these birds. It is possible to derive the Psittacine type as a very apocentric modification of this metacentre, the two anterior loops having become enormously long, and often complicated in themselves, the posterior portion of Meckel's tract being produced also into at least two complex loops, the distal of which is a well-specialized supra-duodenal loop, and the cæca having completely disappeared. However, as the position of the diverticulum is not certain, this derivation of the Psittacine type can be regarded only as provisional. The Striges present a much less apocentric modification of the metacentre. The two anterior loops of Meckel's tract are present, but the second is not so well separated from the general sweep of the tract, and appears to be part of a circular expansion of the whole tract. But in some of the species of *Bubo* the metacentric position is reproduced exactly, and it is easy to regard the conformations in *Strix*, *Syrnium*, and so forth as very slight alterations of the common form. The Meropidæ, the Momotidæ, and the Trogones all retain the metacentric position with extremely little alteration. The Upupidæ, the Alcedinidæ, and the Pici are all apocentric modifications of it, the chief difference being the disappearance of the cæca and the elaboration of a distinct supra-duodenal loop.

#### SUMMARY OF THE SYSTEMATIC DESCRIPTION.

The various conformations of the Intestinal Tract in birds may all be referred to an archecentric form, and this form is well displayed in *Palamedea*. The Struthious birds (with which the Tinamidæ are not included) adhere closely to this archecentric type. The Turnices and the Galli adhere to it almost as closely, but among the Galli an apocentricity, consisting in the expansion of the distal portion of Meckel's tract, begins to appear. The Tinamidæ, the Opisthocomidæ, and the Pteroclo-Columbæ present apocentric conformations which are not easy to derive from those in any other groups, although there are certain suggestions of affinity with the type displayed by Gruiform birds such as *Otis*. For the present, however, it is preferable to regard the forms in these birds as separate, although allied derivatives of the central type. The Passeres again do not show any clear affinity with the types in other birds. The conformation displayed must be regarded as having come separately from an archecentric type, perhaps from that common to the other Coraciomorphine birds, but which has progressed very far apocentrically along a radius of its own. The conformations in all other birds may be referred without difficulty to three main metacentres, which are all simple, but different modifications of the archecentric type. The metacentre of all the birds in the Pelargo-Colymbomorphine Brigade is a conformation in which the

symmetry of Meckel's tract about the median mesenteric vein and the Meckel's diverticulum is retained, but in which Meckel's tract tends to be produced into a number of long and narrow loops, the most distal of which is a supra-duodenal loop to which the long cæca are attached. The metacentre of the Limicoline-Gruiform assemblages (which contains the Alectoromorphine Legion without the Tinamiformes, Galliformes, and Pteroclo-Columbæ) is a derivative of the archcentre in which Meckel's tract is no longer symmetrical about the middle mesenteric vein and the diverticulum, but in which the region anterior to the diverticulum is produced beyond it so as to form an axial loop, on the distal limb of which the diverticulum lies and which may be greatly

Fig. 75.



Evolution of the Intestinal Tract in Aves.

(For Coraciomorphine and Colymbimorphine read Coraciomorphine and Colymbomorphine.)

prolonged as in *Scolopax*. The members of the Coraciomorphine Legion, except the Passeres and a few pseudocentric types, may be derived from a metacentre in which the duodenum tends to widen, and in which the part of Meckel's tract anterior to the diverticulum is produced into two loops. In Plates 21, 22, and 23, and in figures 33, 59, 74, and 75, the evolution and affinities of the conformations of the intestinal tract are represented, and by no means necessarily the pedigrees and affinities of the birds containing these conformations.

#### INTESTINAL PORTION OF THE AUTONOMIC NERVOUS SYSTEM.

It was only at a late stage of this investigation that my attention was directed to the peculiar features in the Sympathetic, or, to use the modern term, the Autonomic Nervous System of Birds. In certain birds (for instance the Megapodidæ and Cracidæ) the

so-called intestinal nerve is unusually large and visible, and it was in members of these families that I first noticed it. In the majority of cases, however, it is not readily seen; moreover, much of my material consisted of rather badly preserved spirit-specimens, or of birds that had died of disease in which tubercular and fatty degenerations of the mesentery were a conspicuous feature, and I am able only to give a few almost casual notes, which, however, may serve the purpose of redirecting the attention of anatomists to a very peculiar and interesting set of structures. A good deal is known about the paired ganglionated mesenteric chain (*Grenzstrang* of the German writers), thanks to the observations of many writers, of whom the chief are Wiedersheim, Gadow, Gaskell, and Marage. In the cervical region [Wiedersheim (36. p. 350), Gadow (12. p. 394), and Marage (23, *passim*)] it divides into a deep and a more superficial portion, and irregular traces of this division persist in different birds in the posterior parts of the body. In all cases it appears to have more autonomy; that is to say, to be in less intimate connection with the metameric spinal nerves than in most other vertebrate forms. In the lumbar region there arises from this a very complex plexus with large ganglia on the edge of the stomach, on the ovary, on the supra-renal capsule, and further back near the rectum. It is from these ganglia that the so-called intestinal nerve of birds arises. Concerning this peculiar nerve the literature is very scanty. Remak (32, 33) appears to have called attention to it first, but most later writers pass it over almost completely. Thus Gadow, Wiedersheim, Fürbringer, and Beddard, in their ornithological and anatomical treatises, pass it by. Oppel, in his great work on the anatomical tract (30), is content with discussion of the plexuses actually in the wall of the gut. Gegenbaur (14), in the most recent edition of his 'Text-book,' mentions the existence of such a nerve in reptiles, and states that it is best developed in birds ("Am meisten sind diese Nerven bei Vögeln entwickelt. Ein den Mitteldarm begleitender Nervenstamm geht am Enddarme in mehrere ansehnliche Ganglien"), and adds that it is undeveloped in mammals. Marage (23) has given the best account of it, and states that it differs in its arrangement in different birds; but his figures are rather difficult to follow, and he is incorrect in stating that it does not occur in rapacious birds, and he seems to have overlooked it in the Ratites. As I have already stated, I do not pretend to have made anything that approaches to a complete study of it, and the figures that I have been able to give must be taken only as rough anatomical notes. Special study by special methods on material in good condition is required\*. I can say, however, that in every case since I was aware of its existence, where the material was in sufficiently good condition, I found it present, and I do not doubt that this presence is invariable. It arises usually from two or three main nerves, which leave the ganglia corresponding to the solar plexus and the ganglia over the ovary and supra-renal capsule, and enter the mesenteric expanse which is the support of Meckel's tract. These, or some of these, are represented in figures 1 and 45, and I have worked them out in several unfigured cases. In fig. 72 there is a

\* Since writing this memoir, my attention has been directed to a beautiful memoir by Thébault (34), which contains, *inter alia*, an elaborate study of the modes of origin of the intestinal nerve in various types of birds.—  
P. C. M.



large ganglion at entrance of these to Meckel's tract, and I could make out only two nerves forming the origin of this ganglion. One of the three nerves frequently runs independently to the duodenum, as in *Otis* (fig. 45) and in *Andigena Bailloni*; but no doubt there may have been a cross connection between this and the main intestinal nerve, as certainly is the case in the Pigeon. In the duodenal-fold loop usually at least one distinct and large ganglion is present (fig. 45, *v.n.r.*; fig. 72, *d.g.*). The main intestinal nerve which supplies Meckel's tract starts in common with the duodenal nerve as in *Palamedea* (fig. 1) and the Passeres (fig. 72). It courses round the mesenteric expanse of the tract, giving off a series of minute branches to the gut, and where the tract passes into the rectum it frequently receives one of the entering nerves, or is in connection with the ganglion at the entrance to the mesentery of Meckel's tract, and then turns down parallel to the rectum, and comes again into connection with the posterior portion of the Grenzstrang. On its course this main intestinal nerve may follow Meckel's tract more or less closely. Thus in *Palamedea* (fig. 1), *Pandion* (fig. 34), *Talegallus* (fig. 38), it forms a loop corresponding to, but not absolutely identical with, the course of the tract. In *Falco melanogenys* (fig. 32) it follows the general course of the tract much more closely, having a loop following the supra-duodenal loop. In *Crax Daubentoni* (fig. 39) it has a curious elongated and narrow distal portion, which corresponds exactly with the typical apocentricity of these birds, in which the tract itself is enlarged on its distal portion. This intestinal nerve in many cases—Struthious birds, *Palamedea* (fig. 1), *Talegallus* (fig. 38), *Crax* (fig. 39), other Galli, *Falco* (fig. 32), *Pandion* (fig. 34)—presents a very large number of small ganglia evenly distributed along its course. In other birds, e. g., *Otis* (fig. 45), *Columba*, *Andigena*, and *Corvus* (fig. 72), there are a smaller number of much larger ganglia. As to the systematic value of these differences, it is impossible to say anything definite on so small a range of information; but the subject is very promising. It appears as if the chain with many ganglia were more primitive than the nerve with a limited number of large ganglia; and it is certainly the case that such birds as *Otis*, *Columba*, the Toucan, and the Passeres, where the number of ganglia is very small, are more specialized forms than those with multi-ganglionated chains. It has to be remembered, however, that although the nervous systems of many invertebrates with a small number of large ganglia appear to have been produced by the concentration of multi-ganglionated chains, we have no right to extend such a principle to other forms. The origin of this intestinal nerve in birds requires to be worked out, and in this connection the observations of Andersson (1), who found that in the Urodele Amphibia the main sympathetic chain was subdivided into a *Grenzstrang* and a *Collateralstrang*, are worthy of attention.

It is to be noticed that this intestinal nervous system lies, as the blood-vessels lie, between the two layers of the mesentery, and therefore outside the cœlom. In larger forms, such as the Emu, it is often comparatively easy to strip off one layer with its load of fat from the mesenterial expanse supporting Meckel's tract, upon which the ganglionated nerve-chain come plainly into view. However, just as it occasionally happens that some of the blood-vessels pierce the mesentery and form "bridging" vessels traversing the portion of cœlom between two loops which happen to lie in contact, so in



certain cases nerves may "bridge," or rather bore through, the mesentery and pass across a narrow portion of coelomic space. The most obvious case of this occurrence is where, as in *Otis*, nerves leave a ganglion in the duodenal loop and pass to the cæca or the supra-duodenal loop. I am practically certain that this happens in many of the small Passerines, where the supra-duodenal loop is a structure of considerable importance, but I am not yet prepared to demonstrate this.

#### MORPHOLOGY OF THE INTESTINAL TRACT.

The chief writers on this subject within comparatively recent times have been Toldt (35), who deals chiefly with the tract in Man; Klaatsch (18), who in two extremely important memoirs dealt with the relation of the tract and its ancillary viscera to the mesentery; and Mathes (24), who followed closely the work of Klaatsch, but dealt chiefly with the development of the mesenteries in the Amphibia. None of these writers has paid special attention to the conditions that exist among Birds, but their work has been of great assistance to me in interpreting and coordinating my own investigations. It is plain that in all the higher vertebrates the intestinal tract is thrown into three main portions which are homologous throughout the series. Of these, the first is the Duodenum, which in birds is always a closed loop lying ventral to the rest of the tract. It arises extremely early in ontogeny, and while in the majority of cases it remains simple, it may develop many minor complexities, sometimes simply becoming wider, sometimes being thrown into numerous minor folds, and sometimes being twisted into more or less regular spirals, the spiral duodenum being in some cases (Storks) wound with the spirally twisted proximal loop of Meckel's tract. Concerning the relations of the duodenum to the supra-duodenal loop I shall presently have more to say. The distal extremity of the duodenum, however the course of that may have been complex, always returns to the dorsal edge of the mesentery very close to the starting point of the anterior limb, and there passes into the second portion of the gut. This portion, which I name Meckel's Tract, extends from the duodenum to the insertion of the cæca. The first important point about this large region of the gut is that it represents an outgrowth of only a very small section of the primitive gut. Its proximal extremity approaches its distal extremity so closely in the line of the dorsal attachment of the mesentery, that in the majority of cases it would be possible to remove the whole of Meckel's tract and suture the cut edge of the duodenum to the cut proximal edge of the rectum, and almost without dislocation reconstruct a primitive straight intestinal canal. In actual development Meckel's tract, in all the vertebrates in which it is developed, arises as a simple narrow loop in the line of the principal mesenteric artery. Toldt's figures, and others given by Kollman (19), show this beautifully in the case of human embryos, and general comparative anatomy from the Frog to Man makes the morphological nature of Meckel's tract extremely plain. There can be no doubt that this is the most recent phylogenetic development of the Vertebrate gut, and that it corresponds to not more than two, or possibly three, of the primitive somites of the body. When the development and comparative anatomy of the intestinal nervous chain in Birds has been worked out,

it is to be expected that the origin of that system from not more than three entering nerve-branches will be given an importance which as yet can only be suspected. The nature of Meckel's tract as a recent outgrowth of a portion of the gut corresponding only to a very limited number of segments has an important bearing on medical work, as it is being found that there is an organic sympathy through the nervous system between certain superficial areas of the skin and certain visceral organs or portions of the organs; the sympathy depending on a common relation to the primitive segmentation of the body, and being of practical value in the diagnosis of affections of internal organs. In those creatures in which there is a yolk-sac or umbilical cord, the outgrowth of Meckel's tract from the primitive straight gut is opposite the vessels running to these structures; and it seems tempting to regard the origination of Meckel's tract as being dependent on this mode of embryonic nutrition. However, as Meckel's tract is equally definite and equally metamerically limited in the Frog, we cannot lay much stress on this possible mode of origin.

The large intestine, from the cæca to the cloaca or anus, is the third distinct portion of the intestinal tract. It always lies in the primitive position of the straight gut, dorsad of all the other portions, and phylogenetically it is the oldest portion and corresponds to the greatest number of somites. It appears to be homologous throughout the vertebrate series; but this homology depends on the identification of the paired cæca of Birds with the unpaired cæcum of Mammals and Lizards—a homology not apparent when a bird with a short gut is taken, but much more convincing when the comparison is made between a form such as *Palamedea* (fig. 1) or a Struthious bird and a Mammalian or Lacertilian intestinal tract. In the more primitive types the large intestine is very long, and may show traces of division into colon and rectum; in the higher forms, partly in correlation with the greater development of the thoracic portion of the viscera, the duodenum and whole intestinal tract has shifted far distally, with the result that the large intestine is extremely small, and is here referred to simply as rectum (see footnotes, pp. 176 and 271).

#### MECKEL'S DIVERTICULUM.

Examination of the embryo of any bird makes it plain that this structure is the vestige of the yolk-sac, and its retention in adult birds has been described by a number of anatomists. It has been termed by most writers who understood its nature the *Diverticulum cæcum vitelli*; but as it is obviously homologous with the cæcum described by Meckel as an abnormality in Man, and as in human anatomy it bears the well-known name of Meckel's diverticulum, I have preferred to give it that name in birds. I have not found it present in any adult reptile, and I can find no record of its occurrence there. Nor have I found it in any mammal other than Man. In human anatomy its frequency of occurrence has received recent attention, and Birmingham (4) states that it is present in about 2·2 per cent., varying from half an inch to five inches in length. In birds it is present much more frequently; indeed, its presence throughout life is a character of very many groups. Gadow (12), summing up his own very numerous observations and those of earlier writers, states that it is retained throughout life by

Swimming-birds and most Waders, but that it disappears very early in Birds of Prey, Parrots, Woodpeckers, and Singing-birds. He regards it as a functionless rudiment. Lönnberg and Jägerskiöld (21) examined a large number of birds, chiefly Sea-birds and Waders, for it, not contenting themselves with single individuals, and found it absent in most Gulls and Terns, present in Waders, Ducks, Herons, and some others. As at an early stage in my investigations I found it an important point of morphological orientation, I searched for it in each of the very large number of birds upon which this communication is based, and found its presence much more frequent than has been stated. An interesting feature in connection with it is, that in a large number of cases it is supported by a vestige of the primitive ventral mesentery. Usually this appears only as a small fold of tissue tying down the diverticulum to the ventral edge of the gut, but sometimes a strong band runs from this towards the liver, the latter of course being developed in the primitive ventral mesentery. Occasionally when the diverticulum itself was absent, its place was indicated by the presence of a mesenterial vestige, as in many Pigeons.

I have found the Diverticulum present and large in all the Ratitæ; of the Colymbiformes absent only in *Podiceps*; present in the Sphenisciformes; present in the Procellariiformes; of the Ciconiiformes, present and large in all the Steganopodes but small in *Plutus*, and present and large in the Ardeidæ, Scopidæ, Ciconiæ, and Phœnicopteri, in many of the Ciconiiformes being very large: present and large in all the Anseriformes; present in all the Falconiformes (except a *Buteo*), and very large in the Falconidæ, but usually small in the others; present and large in the Tinamiformes; present but usually very small in the Galliformes (except *Turnix*); present and very large in all the Gruiformes, often extremely large, but, as a solitary exception, absent in *Heliornis*; present and very large in all the Limicolæ; among Lari small and often absent in the Laridæ, small, but usually present, in the Alcidæ; present in the Pterocletidæ, but usually absent and always extremely small in the Columbidae, a feature in which they stand in marked contrast with the Charadriiformes generally; of the Cuculiformes, always present although small in the Cuculidæ; absent in the Musophagidæ, and probably always absent in the Psittaci; of the Coraciiformes, always small, but present rather more often than not in the Coraciæ, present and small in most of the Striges, very small but present in most Caprimulgi; always very small and absent more often than present in the Cypseli, Colii, Trogones, Pici: of the Passeriformes, absent in the vast majority of cases, when present extremely small except as a solitary case in *Menura*, where it was very large. In making this review I have excluded those specimens which were marked in my notes as obviously chicks or quite young birds, and the list may be taken as representing with fair exactness the incidence of the diverticulum among the Avian groups.

In all the cases where I have mentioned, in the paragraph above, that Meckel's diverticulum was *small*, I think that it was a vestige in the true sense, that is to say a functionless rudiment of an embryonic structure. Sometimes the lumen remained, and contained a few fragments of material resembling yolk, and doubtless remains of the yolk. Rather more frequently the "small" diverticula had no lumen, and were mere nodular excrescences on the wall of the Tract. Among the cases which I have noted as large there are certainly some (Ratites, *Palamedea*, etc.) in the same category. The curious feature

therefore exists that a functionless vestige is retained universally in some groups and not in other groups—a circumstance to which the attention of those naturalists may be directed who would see a purpose or “selection-value” in every systematic character.

Meckel's diverticulum presents another condition of great interest. Lönnberg and Jägerskiöld (21) drew attention to the fact that in certain cases where the diverticulum is large, it has a patent lumen and a thick wall, and is slightly constricted from the gut (21, cited in Oppel 30, p. 559). These authors, while they suggest that the vestigial organ has been transformed into a gland, do not go further in their microscopical investigation than to point out that the mucous membrane of the diverticulum in these cases is thickened by a series of folds. I have examined the microscopical structure in several Anatiformes, Gruiformes, and Charadriiformes, and find that glands occur frequently in the foldings of the mucous membrane, and that the diverticulum in such cases corresponds, with its folded wall containing glands and lymphoid nodules, very closely to the structure of the cæca in Passerines and Columbæ. I am inclined to think, therefore, that in many cases, particularly in the groups that I have mentioned (and possibly in the Falconinæ), Meckel's diverticulum has acquired a new function. It is at the least suggestive that where the diverticulum has become glandular, the paired cæca are either rudimentary and functionless, or they are very large, thin-walled, and full of faecal matter. Where, on the other hand, the paired cæca are chiefly glandular, the diverticulum is either a functionless vestige or has disappeared. This, however, is not a complete account of the relations of the two organs; for, in the first place, it is based only on a relatively small number of observations of microscopical structure, and in the second place there are instances, such as the Psittaci, where both diverticulum and paired cæca are absent in the adult.

#### THE SUBSIDIARY LOOPS OF MECKEL'S TRACT.

In the section dealing with systematic description, I have already said all or nearly all that I have to say regarding the minor loops into which the Tract so frequently is produced. I have tried to show that these display patterns which persist through systematic groups, the persistency referring to their position with regard to the diverticulum and to their number. The arrangements of these minor loops, in fact, are instances of what I term uniradial apocentricities. When Meckel's tract is elongating, in a large bird or in a bird the habits of which demand a great length of gut, the elongation does not take place at random, but in special regions and in special modes. The combination of position and complexity is of a kind not likely to be repeated independently, but to have common origin, and so to prove of systematic value. The explanation of how these different and complex combinations came into existence I have not attempted. Before that could be done, there is necessary the great labour of following out in every stage of individual development the relations of the growing folds of the gut to the blood-vessels, regions of the cœlom, liver, air-sacs, sternum, stomach, and so forth. The beautiful work of Klaatsch and of Mathes, elaborate and prolonged as it was, does little more than to open up the lines of such enquiries. Until something is known in each individual case of the nature of the “growth-forces” in contiguous

organs, of their compromises and co-ordinations, in fact of their places with regard to one another and to the whole corporeal republic in every stage of the growing embryo, nothing more can be said but that such complex uniradial apocentricities, if not in themselves possessed of "selection-value," may stand in correlation with structures that have such value.

#### THE SUPRA-DUODENAL LOOP.

In its natural condition the duodenum lies folded ventrally under the other portions of the gut, and comes in very close relation with the distal portion of Meckel's tract. Cuvier drew attention to the fact that in birds as in mammals the duodenum comes into intimate relation with a posterior portion of the gut, a relation so intimate that the mesenterial folds suspending the two portions may fuse after the fashion explained by Klaatsch. This portion of the gut which comes into relation with the cæca I have called the supra-duodenal loop, preferring not to call it "colon" as was done by Cuvier, since that term is applied in Mammalian anatomy to a portion of the gut posterior to the cæca, and therefore belonging to what I have been terming the rectum. Within the group of birds various stages in the evolution of this curious inter-relation between the proximal and distal portions of the gut are displayed. Thus in *Palamedea* (fig. 1) there is no supra-duodenal loop, and the gut may be unfolded without any difficulty or cutting of blood-vessels. The same conditions obtain in a number of the archecentric types, and in the systematic portion I have referred to these. Even in *Palamedea*, however, the earliest stage in the formation of the connection is apparent. A short recurrent factor of the duodenal vein runs in the mesentery at the dorsal portion of Meckel's tract across from the terminal portion of that tract and assists in draining the cæca. As the cæca increase in size this vessel becomes larger and of more importance, and, in many cases which I have referred to in the systematic portion, the recurrent vein along with a second and sometimes a third accessory recurrent vein run to nearer the apex of the duodenum, having traversed the mesentery as "bridging" veins, and arisen from the long cæca and the posterior portion of Meckel's tract. In such a mode, an intimate relation is established between the duodenum and the distal portion of Meckel's tract, and, as in *Olin*, this relation may involve not only the veins but the nerves. The portion of the Tract to which the cæca are adherent is not distinctly marked off from the more proximal portion of the Tract in very many of the less apocentric types. But, as I have shown in the systematic portion, *pari passu* with the establishment of the "bridging" veins, the distal portion of the Tract becomes a distinct loop clearly marked off from the general sweep of the Tract. Finally, in those birds where the cæca have degenerated either completely or have shortened to glandular nipples, the supra-duodenal loop is retained with its separateness from the rest of the Tract and with its "bridging" veins. In such a form the supra-duodenal loop generally becomes very accurately moulded to the contour of the duodenum, and its presence and completeness are important reasons for seeing in the apparent simplicity of the gut in many of the higher forms, such as the Passeres, a pseudocentricity—a condition apparently simple, but still retaining evidence of past complexity. I do not think it can be doubted



that wherever in short-gutted birds without large cæca the supra-duodenal loop is present in its elaborate form, these birds at one time had a longer gut, and almost certainly possessed longer cæca. Where a gut is long, and where its irregularly folded loops lie closely together in a narrow space, the establishment of an intimate connection between any of the crowded loops would call for little remark. Where, as in the Passeres and many other short-gutted forms, there appears to be abundant space, and yet the duodenum and the supra-duodenal loop are accurately moulded, the one on the other, and in intimate vascular, nervous, and mesenteric connection, we must seek for the origin of the complexity in the past history.

There can be no doubt, I think, that the presence of a specialized supra-duodenal loop marks a high degree of apocentricity in the intestinal tract possessing it, but it is equally plain that this apocentricity is multiradial and no guide to affinity. The presence of cæca of at least moderate length is a fundamental or archeocentric character of birds; and, if the supra-duodenal loop has arisen in the mode I have indicated, it is clear that it may have arisen repeatedly, and in my systematic description I showed that actually it does appear, repeatedly and apparently independently, in the different groups. The probably multiradial nature of the structure is also supported by the occurrence of similar formations among Mammals, these formations not even being on exactly homologous parts of the gut. The mammalian structures with which the Supra-duodenal Loop may be compared are the loop which in Man has the transverse colon as its apical portion, and the sigmoid flexure, which in embryonic Man reaches much further towards the duodenum. Naturally, I do not propose to enter at present into the various modifications presented by these structures; it is enough to say that the connections in Mammals between the duodenum and posterior regions of the gut are frequently present, but less frequently than in the case of Birds.

Dealing with its occurrence in Man, Toldt sees in these connections between the proximal and distal portions of the gut the mere result of apposition. Klaatsch criticises this view, and rightly points out that, although many of the other loops are in equally close spatial relations, fusion does not necessarily occur among them. In Birds, however, as I have shown, secondary fusions and "bridging" veins are not absolutely confined to the duodenum and supra-duodenal loop. Thus in Psittaci they are frequent among the numerous long and narrow loops into which Meckel's tract is thrown. In Anatidæ secondary fusions and "bridging" veins are of frequent occurrence in the case of different portions of the same loop, notably in the axial loop, and in *Spatula* in the long loop distal to Meckel's diverticulum (fig. 24). Finally, in the Ciconiæ bridging veins and secondary fusion of the mesentery occur between the duodenum and the proximal minor loop of Meckel's tract. These occurrences, however, are less important and much less frequent than the supra-duodenal connections. Klaatsch accounts for these in the case of Reptiles and Birds by the mode in which the cœlomic divisions are broken up by the intruding blood-vessels and viscera. I think, however, that, in birds, the formation may serve a useful purpose; the supra-duodenal loop is maintained and made even more elaborate after the degeneration of the cæca, although it arose in relation to the cæca; moreover, it is specially perfect in cases where there is no reason to

suppose that want of space played a part in its ontogenetic appearance. Plainly, when the pyloric valve relaxes and the contents of the stomach are poured into the duodenum, the shock will be transferred to the supra-duodenal loop which lies closely applied to the duodenum and sometimes in special nerve-connection with it. And thus discharge of the contents of the posterior region of the gut into the rectum may be set about without the necessity of peristaltic waves traversing the whole length of Meckel's tract.

#### THE COLIC CÆCA.

Gadow (12), Fürbringer (9), Beddard (2), and Oppel (30), in their respective treatises have devoted so much attention to the voluminous literature concerning the colic cæca of birds that I need not refer to older writers. The archecentric condition of these organs in birds, a condition which is probably an heritage from Reptilian ancestors, is the existence of a pair of cæca growing from the point where the distal end of Meckel's tract passes into the rectum. Such primitive cæca proximally are applied more or less closely to the posterior portion of Meckel's tract. They are of moderate length; their walls are not specially thickened, their lumens are widely open to the gut, and their contents consist of food-material in a state more akin to that in the rectum than to the state in Meckel's tract. When, as happens frequently, there is a difference in colour apparent through the intestinal wall and marking the different stages of metabolism, the colour of the cæca approximates to that of the rectum. These primitive cæca probably had a digestive function of some sort, for the presence in their walls of glands, of absorbing veins, and occasionally of villi show that they were not mere reservoirs of faecal matter. From the primitive condition various apocentric modifications have arisen. The cæca may increase very greatly in size, and may develop spirally arranged septa protruding more or less into the cavity and deeply marking the exterior, as in *Chauna* and some of the Ratites and Gruiformes, or the whole external surface may be prolonged into a number of papilliform hollow outgrowths, as in *Calodromas* described by Beddard (2). These enlarged cæca appear to retain their digestive functions. Secondly, the cæca may become very much reduced, but in such apocentric reduction I am convinced that there are two quite different conditions to be noted. In the one case, the reduction may be nothing more than the degeneration of an organ that has become functionless; and almost any stage from the archecentric size to complete absence may exist. In the Columbidae, for instance, the cæca if present are always small and frequently are thin-walled, irregular (I have noted many cases of individual absence of one cæcum), and sometimes pigmented. In the fruit-eating Pigeons, and indeed in many other Pigeons apart from the nature of their food, the vestiges have disappeared completely. Precisely a similar series of events occurs among most Falconiform birds. The cæca are small in all, and when present appear to be functionless, thin-walled vestiges, frequently unsymmetrical (here, again, absence on one side has been noted in different birds by different observers). Sometimes they appear to be absent, but inflation of the wall of the gut reveals the presence of slight, thin-walled rudiments in their place. In the Vultures they are sometimes totally absent, and a similar absence is a



character of the Cathartidæ. However, there is yet another condition possible among these reduced cæca. Numerous observers have shown that in the cæca of many birds, whether these be long or short, there occur in different regions masses of lymphoid tissue. Such masses may occur at the apex of long cæca as in the Owls, or in scattered patches as in Ducks and Fowls, or in concentrated swellings as in *Otis*. Berry (3) has recently shown that the occurrence of these lymphoid masses, in concentrated regions forming vermiform appendices, or in scattered masses, is frequent in Vertebrates, and he suggests that the vermiform appendix of Man is a specialized and not a degenerate structure. The reduced cæca of many birds (*e. g.* Passerines) are quite different from the obviously vestigial cæca that I have mentioned. They are regularly formed, nipple-like structures, the lumen of which is greatly reduced by closely-set villi and folds. In these, small glands and lymphoid tissue are abundant; and in the Sparrow I have noted the presence of abundant dark granules which are apparently matter in process of excretion. I distinguish therefore in the conditions of the cæca among birds the following:—

1. *Archecentric Character*.—Cæca large, thin-walled, containing food-material on which some process of digestion is taking place, but which may have in addition the beginning of secretory or excretory function.
2. *Apocentric Characters*.
  - A. Cæca enlarged, partly digestive, and partly secretory or excretory.
  - B. Cæca functionless, vestigial or absent.
  - C. Cæca reduced but transformed solely to glandular organs, secretory or excretory or both.

PALAMEDEA. Cæca archecentric. *Chauna* apocentric A.

RATITÆ. Cæcæ archecentric or apocentric A.

COLYMBIFORMES. Archecentric.

SPHENISCIFORMES. Apocentric B. but according to Gadow archecentric in some.

PROCELLARIIFORMES. Apocentric B, occasionally one only present.

CICONIIFORMES. Archecentric in the Pelecanidæ, apocentric B in the Phaethontidæ, Sulidæ, Fregatidæ, and Phalacrocoracidæ (in *Plotus* one may be absent); apocentric B in the Scopidæ, Ciconiidæ, and Ardeidæ, in the latter one only as the normal but not invariable condition. In the Phœnicopteri archecentric.

ANSERIFORMES (excluding the Palamedeidæ). Apocentric A, usually with large rows of glands, but in *Mergus* apocentric B and one occasionally absent.

FALCONIFORMES. Apocentric B, vestigial with frequent irregularities and absent in Cathartidæ.

TINAMIFORMES. Apocentric A, extreme specialization in some.

GALLIFORMES. Apocentric A in Galli and Opisthocœmi; archecentric in Turnices.

GRUIFORMES. In the Rallidæ apocentric A; of the Gruidæ archecentric in the Araminæ, apocentric A in the others. In the Dicholophidæ and Otididæ apocentric A (extremely so in *Otis*); in the Rhinocetidæ archecentric; in the Eurypygidæ apocentric, probably C; in the Heliornithidæ archecentric.

CHARADRIIFORMES.

*Limicolæ*. In the Glareolidæ archecentric; in the Chionidæ, Thinocoridæ, and Charadriidæ apocentric A, but in some of the latter family apocentric C. In the Parridæ, Alcridæ, and most of the Laridæ apocentric B and sometimes practically quite absent, but in *Stercorarius* archecentric.

*Pterocletidæ*. Apocentric A.

*Columbidæ*. In the vast majority apocentric B, occasionally one and very often both absent, but in *Columba livia* and *Columba ænas* traces of glandular structure and so apparently apocentric C.

CUCULIFORMES.

*Cuculi*. Archecentric to apocentric A in the Cuculidæ; in the Musophagidæ apocentric B, and usually, if not always, quite absent. In the Psittaci apocentric B.

CORACIIFORMES. In the Coraciidæ, Momotidæ, and Meropidæ archecentric; in the Alcedinidæ and Upupidæ apocentric B.

*Striges*. Apocentric A.

*Caprimulgi*. Archecentric.

*Trogones*. Archecentric.

*Cypseli*, *Colii*, and *Pici* are apocentric B.

PASSERIFORMES. All that I have examined are apocentric C.

Gadow (12. pp. 688-693) has made a very careful study of the relations between the character of the cæca and the nature of the diet, and I have gained further information from Finn (8) and from Evans (7), and from the keepers at the Zoological Gardens as to the diet of birds. There is very far from an exact correlation between the apocentricities and particular diets, but there is enough to make it plain that many of the modifications are homoplastic; that is to say, that they are multiradial apocentricities on which no argument as to affinity can be based.

*Archecentric Type*.—The diet in these forms is by no means uniform, but there is a preponderance of feeding on insects and caterpillars, grubs, and so forth; in fact, of what may be taken as more typical reptilian diet.

*Apocentric Type A*. A very large number of birds displaying much enlarged cæca live on vegetable diet in which cellulose bulks largely, and it is to be remembered that the digestion of cellulose occurs in the large cæca of some mammalia.

*Apocentric Type B*. Carnivorous diet, piscivorous diet, and especially frugivorous diet are specially associated with the degeneration of the cæca to functionless vestiges, or even with the complete disappearance of the cæca.

*Apocentric Type C*. When it is remembered that the vast majority of the Passeres display this type, and that yet almost every possible form of diet is found among them, it is at once clear that diet is no complete explanation of the character of the cæca. I am more inclined to think that type C is to be associated with a high development of the Avian structure, and that it is a peculiar secretory or excretory organ.

Some parallels may make the complexity of the problem of the cæca apparent. The Passeres display all diets and one type.

The Owls and the Falconiformes have almost identical diet, the larger forms of both being carnivorous, the smaller forms chiefly insectivorous; the Owls all exhibit apocentricity A, the Falconiformes apocentricity B.

Fowls and Pigeons (except the fruit-eating Pigeons) have a similar diet; Fowls all exhibit apocentricity A; Pigeons apocentricity B or rarely C.

The Gulls have a similar diet consisting of fish and garbage; most exhibit apocentricity B, but *Stercorarius* is archecentric.

On the other hand, *Phænicopterus* is distinguished from other Ciconiiformes by a nearly purely vegetable diet, and it has the longest cæca in the group. The Mergansers are distinguished from the other Anatidæ by their typically piscivorous diet, and they alone among the Anatidæ have apocentricity B as in most other fish-eaters.

#### CHARACTERS AND CLASSIFICATION.

In the systematic descriptive part, my task was to treat the characters of the patterns displayed by different birds as nearly as possible as if the gut were the whole animal, and the various phylogenetic figures and the three Plates display what I take to be the relations of the intestinal tracts, and not necessarily the relations of the possessors of these tracts. I have been taking, in fact, the anatomical structure as the unit, and not the individual or the species. In a sense, this is a return to the old Hunterian method; but its purpose reflects on the new problem of the nature and evolution of varieties and species of genera and families. Granting that the Plates attached to this paper represent with approximate accuracy the phylogeny of the intestinal tract in birds, we have yet to learn the relation of the phylogenetic tree of this structure to the phylogenetic trees of other structures, and the relation of all these to the phylogenetic trees of these impermanent combinations of characters that we call species. Although the coincidence of such trees is frequently assumed, there is no *à priori* reason to support such a proposition; and there is much recent work on the nature of characters and of their inheritance to throw doubt on the proposition. The nature of the anatomical structure in any organism depends in the first place on the nature of certain material transmitted from the parents in the fertilized ovum (naturally it does not matter to the argument whether the transmitted substance be what we call "matter" or "state of matter" such as mode of rhythm). Among other writers de Vries (6) has recently brought strong experimental evidence to show that at least in plants the hereditary material is composed of independent units which may be sorted out and recombined in each sexual generation. Of such independent variables underlying the fully developed anatomical structures of animals, we know practically nothing as to their number, nature, or modes of sorting out and recombination as they pass from generation to generation. Next, the anatomical structures of animals depend on the environment in which the combination of transmitted units come to maturity as actual adult organs; that is to say, they depend on the

various correlations with other organs and with external conditions established during embryonic, youthful, and adult life. In the case of the alimentary canal we know just enough, from the transforming experiments of Hunter and others, to feel certain that a large part of the final structure is determined by the conditions in which the hereditary material is grown. The phylogenetic tree of an organ such as the alimentary tract may be little more than the exhibition of a long series of experiments in growing similar or identical "germs" in different culture media. And, finally, we know nothing as to how far these hereditary masses, as they were marshalled into the actual branches of the actual phylogenetic tree of the organisms that contained them, carried within themselves historical limitations or determinations towards further development in specialized directions.

Such questions, however they may seem remote from an actual study in comparative organogeny, in reality lie at the root of every attempt to use characters in classification: if by classification there is implied more than the convenient disposal of particular animals in particular pigeon-holes according to their possession of obvious anatomical characters. The study of characters by themselves and for themselves must precede the attempt to use these characters in genealogical classification.

In the study of characters, the first proposition is whether they are primitive or modified, archecentric or apocentric. So far as the subject-matter of this paper is concerned, I have tried to show that for Aves the presence of a specialized duodenal loop, of a Meckel's tract consisting of a nearly circular expanse of mesentery with a simply convoluted gut suspended at its periphery and symmetrical about a median vein running towards a vestige of Meckel's diverticulum, of a pair of colic cæca with free lumen of moderate length and with walls partly glandular and partly absorbing, and of a rectum relatively long, are archecentric characters. When birds possess many or even all of these characters, we are tempted to say, but we cannot say definitely, that they are closely akin. The retention by some descendants of a common stock of an ancestral heritage in the ancestral form does not imply that such members are more closely akin than other members that have dissipated or improved the common heritage. I have shown that in all the great accepted groups of birds there are some members with the archecentric condition.

The second proposition that may have to be made regarding characters is that they are modified from the archecentric condition, or apocentric, and in this modification degrees of apocentricity may be exhibited. I have shown that the lengthening and twisting of the duodenum, the appearance of asymmetry in Meckel's tract and its production into variously-formed and variously-placed loops, the special formation of the loops described as supra-cæcal kiuks and supra-duodenal loops, the great lengthening of the colic cæca or their reduction to vestiges or to short compact glands, and the shortening and straightening of the rectum\*, are apocentric characters. That two birds possess

\* Since writing this memoir, I have been interested by noticing that Professor Metchnikoff attributes many of the digestive troubles of man to inheritance of a long rectum. The higher birds of every group apparently have passed through a similar condition, but have succeeded in very greatly reducing the length of the rectum.—P. C. M.

apocentricity in an organ is no evidence of their affinity. In the first place, the apocentricity may be the mere result of growing the same inherited "germs" in similar culture media. I call such apocentricities multiradial, implying that they are the result of similar conditions on the same plastic material. The lengthening of the whole gut and the spiral twisting of portions of it, and in particular the lengthening of the cæca, are plastic or multiradial effects and can have no direct bearing on affinity. The extreme shortening and widening of the whole gut and the disappearance of the cæca, or even their transformation to nipple-like excretory organs, are multiradial. The production of a supra-duodenal loop and its retention after shortening of the long cæca in connection with which it arose are multiradial apocentricities. These again give us no clue to affinity. There is no reason to suppose that even in the actual phylogenetic tree of birds, a branch the members of which now possess an organ with arche-centric character, may not have come from a branch the members of which now possess an apocentric character in the same organ. For, in the first place, the apocentricity may have arisen after the branching; and, in the second place, if the apocentricity be truly plastic, the transmitted germs in another environment may grow only into the ancestral form. It is probable, however, that apocentricities, even if multiradial, leave some legacy of complexity in their simplified descendants, and such conditions of character I have called pseudocentric. The conclusion to which consideration of multiradial apocentricity leads is that even if the phylogenetic trees based on the study of the intestinal tract be absolutely correct, and if they be compared with equally correct trees based on the examination and valuation of other characters, these trees may not coincide.

Apocentricities, however, may be so definite, so precise, or anatomically so complicated, that they appear to imply a phylogenetic contraction of the range of variability in respect to the structure in question. Such a demarcation of modification along a single and definite radius I have called uniradial apocentricity. When further divergent modifications occur on a single radius, there is formed what I have termed a metacentre, and what seems to imply that the range of variability has been limited or defined, with the result that future modifications all retain an indication of their more limited or defined starting-point. I take it that the arche-centre of the alimentary canal of birds is a metacentre of the alimentary canal of the Sauropsida, and that, again, is a metacentre of the alimentary canal of the whole vertebrate stock. I have tried to show that the uniradial apocentricities of the intestinal tract of birds relate to the number and position of the minor loops into which Meckel's tract is produced.

The obvious use of the study of characters as regards classification is, then, the valuation of characters as arche-centric and apocentric, and the discovery among the apocentricities of the uniradial modifications with their metacentres. When these have been determined and valued, the characters have yielded all the material that they afford for genealogical enquiry. When one set has been exhausted, recourse must be made to another set. In other words, the work of the anatomist whose goal is the achievement of natural classification, is the study of the definition and limitation of variation within groups. There is, however, another and most important side to this valuation of

zoological characters. When the archecentricities and apocentricities of a number of organs or structures have been mapped out, the questions are opened as to how far archecentric conditions of different organs are combined in the same animal; how far apocentric conditions are so combined; how far archecentric conditions of one set of structures are associated with apocentric conditions of other sets. In general terms, the problem is how far different organs become modified or remain unmodified independently or in association in the same individuals. If we compare the Dog-fish and the Frog, we find that, in relation to the general characters of the Ichthyopsida, the Dog-fish is arche-centric as regards its skeletal system, apocentric as regards its urinc-genital system, while the Frog is apocentric in its skeleton and archecentric in its urino-genital system. Naturally, in a paper dealing with part of one system, this problem of association has not been raised, but I desire to add my conviction, based on a general study of birds and a particular study of small groups of birds, that the larger the number of forms in a group and the narrower the anatomical range within which the group is confined, the more close is the association of apocentric modification of different organs.

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EXPLANATION OF THE PLATES.

PLATE 21.

Evolution of the Intestinal Tract in the Pelargo-Colymbomorphine Brigade.  
(*For Colymbimorphine read Colymbomorphine.*)

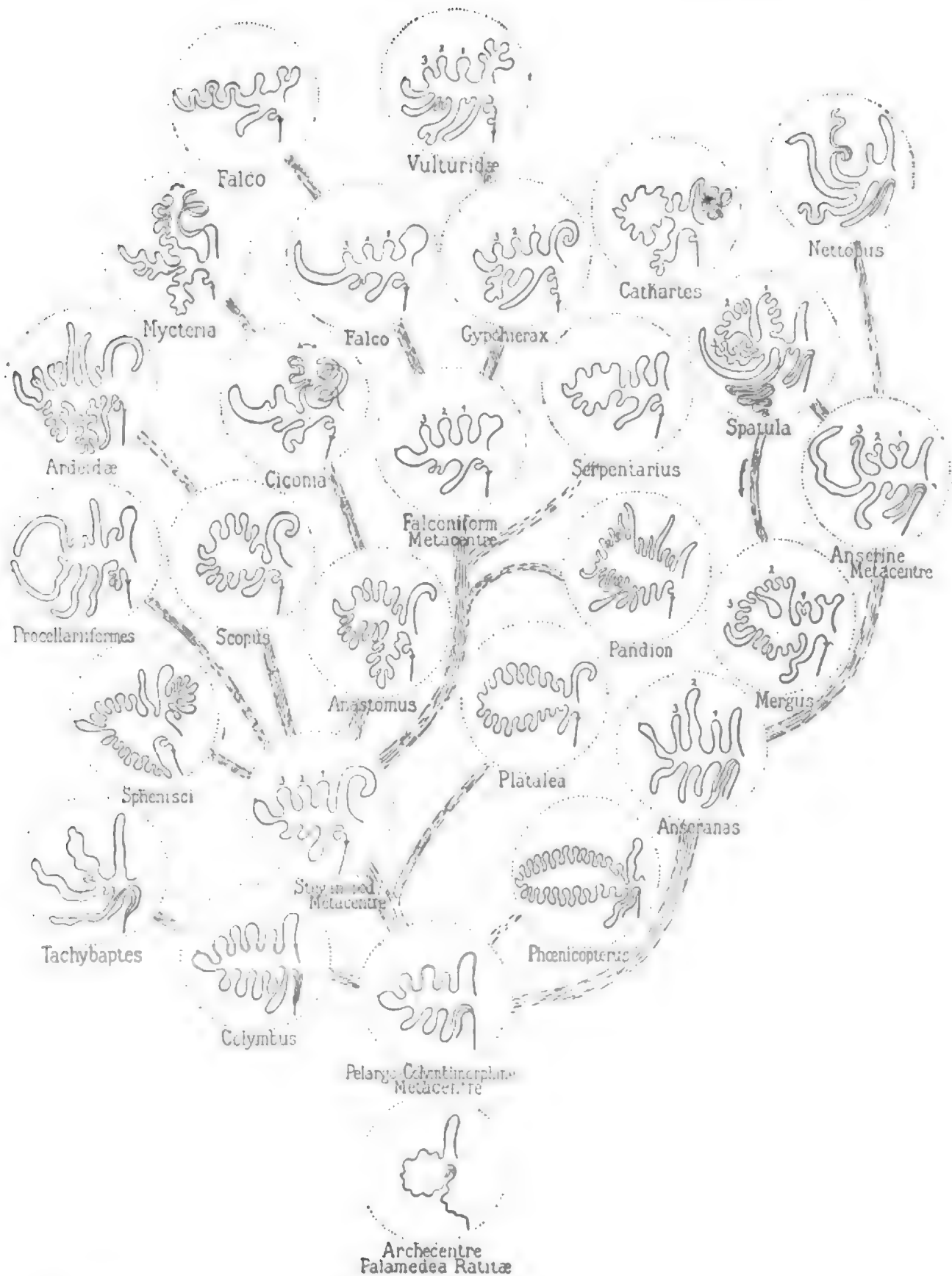
PLATE 22.

Evolution of the Intestinal Tract in the Alektoromorphine Legion.

PLATE 23.

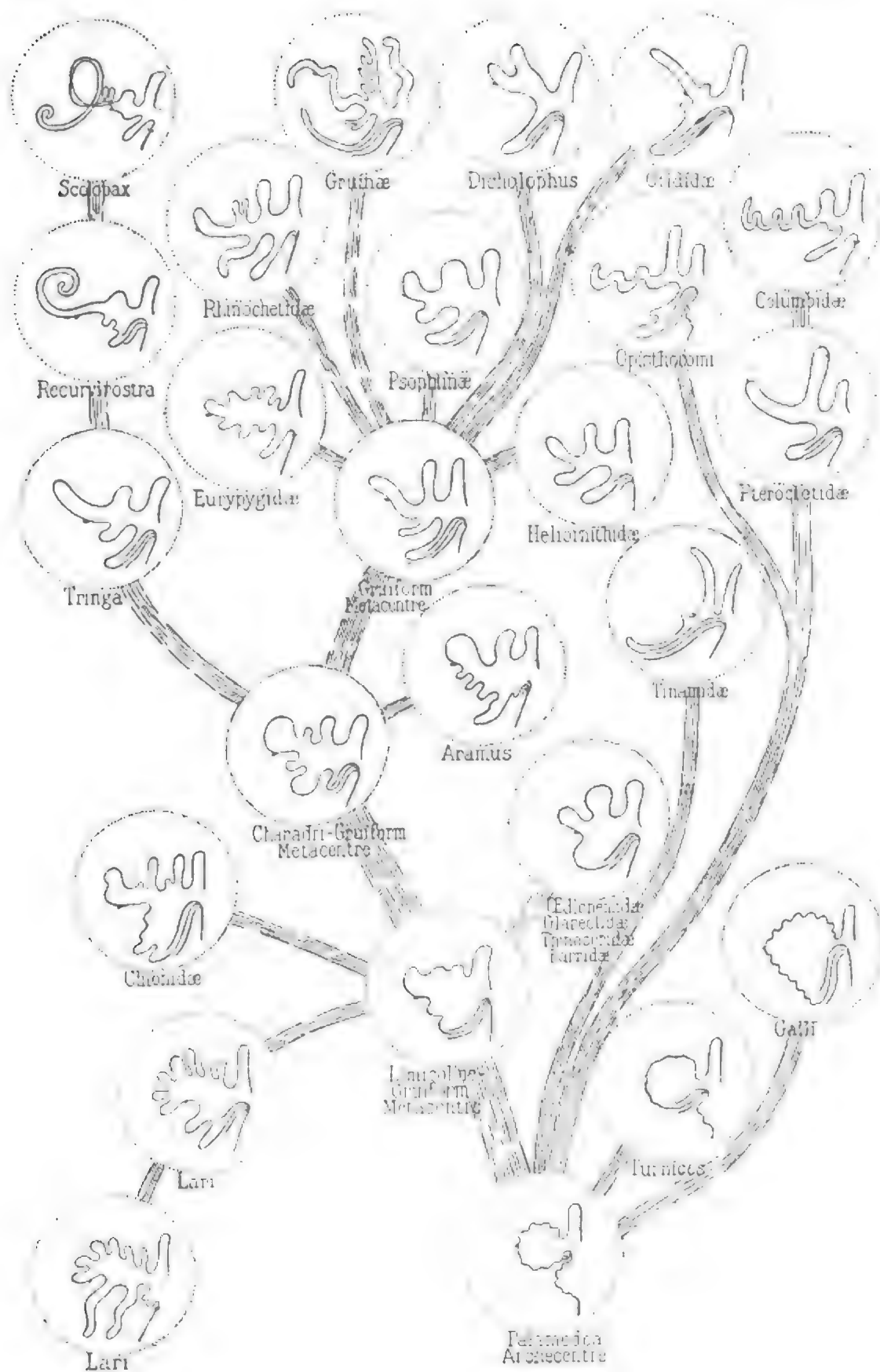
Evolution of the Intestinal Tract in the Coraciomorphine Legion.  
(*For Coracimorphine read Coraciomorphine.*)

In these Plates the affinities of the conformations of the Intestinal Tracts and not of the birds are indicated. The outline of the coils of the tract in the unfolded condition is given; the line of attachment of the mesentery to the body lies to the reader's right. The diverticulum is represented as a dark spot on the left. The duodenum lies towards the upper end of the Plates, the rectum towards the lower end, with the caeca, when present, as a pair of dark lines.



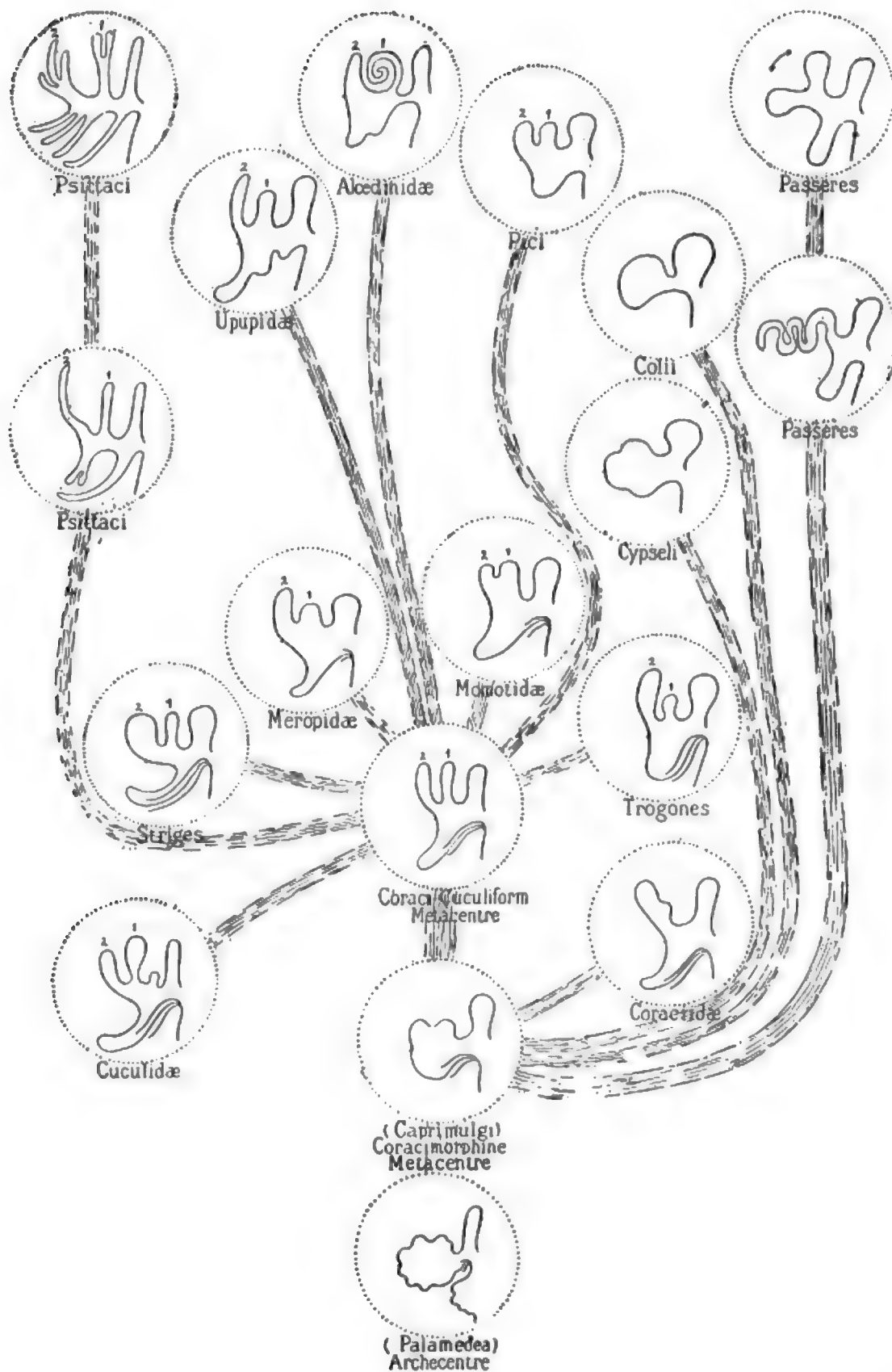
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INTESTINAL TRACT OF BIRDS  
PELAGO-COLYMBIMORPHINE BRIGADE.



INTESTINAL TRACT OF BIRDS  
ALECTOROMORPHINE LEGION





VIII. *Sur quelques Lépadides nouveaux de la Collection du British Museum.*  
 Par A. GRUVEL, Maître de Conférences à la Faculté des Sciences, Université  
 de Bordeaux. (Communiqué par M. le Prof. G. B. HOWES, Sec. Linn.  
 Soc.)

(Planche 24 et 5 figs. dans le texte.)

Lu le 6 mars, 1902.

DURANT le séjour que j'ai fait à Londres, pendant les grandes vacances de 1900, j'avais mis de côté un certain nombre d'échantillons de Lépadides que je considérais comme devant représenter des espèces nouvelles, et que, la durée de mon séjour, malheureusement trop courte, ne me permettait pas d'étudier sur place, d'une façon suffisamment approfondie.

Avec l'autorisation de l'éminent Directeur du British Museum, M. le Prof. Jeffrey Bell eut l'amabilité de me faire envoyer à Bordeaux les échantillons que je lui avais désignés, et c'est le résultat des études dont ils ont été l'objet de ma part, que je viens consigner ici.

Les espèces nouvelles provenant de cet envoi se répartissent en trois genres: le genre *Alepas*, le g. *Pacilasma* et le g. *Scalpellum*.

#### Sous-ordre DES PEDONCULES. (PEDUNCULATA.)

##### Famille des Anaspides. (ANASPIDÆ.) \*

##### Sous-famille des Alépadinés. (ALEPADINÆ.)

##### I. Genre ALEPAS, Sander-Rang, 1829.

Ce genre est un de ceux, peut-être celui qui présente le plus d'uniformité d'organisation parmi les espèces qui le composent. La différenciation à établir entre elles est d'autant plus délicate que ces animaux, étant, soit entièrement privés de plaques capitulaires, soit réduits simplement à des scuta cornés, sous cuticulaires, et sans forme bien définie, n'offrent souvent que des caractères extérieurs peu nets et variables d'un

\* Bien que le genre *Anaspides* ait été créé par G. M. Thomson pour un type nouveau de Schizopode (Trans. Linn. Soc., 2nd ser. Zool. vol. vi. part 3, August 1894), le nom de *Anaspides* me semble pouvoir être conservé pour une famille de Cirrhipèdes.—A. G.

échantillon à l'autre d'une même espèce. Il faut donc, dans la plupart des cas, s'attacher plus encore aux caractères fournis par l'animal lui-même, que par ceux donnés par la forme du capitulum et du pédoncule, et ces caractères internes sont eux-mêmes, parfois si peu nets, que la difficulté pour caractériser nettement les espèces en est ainsi singulièrement augmentée.

Ainsi par exemple, entre les deux espèces que je vais décrire, *A. Belli* et *A. microstoma*, il existe des différences très nettes, qui m'ont permis de les séparer, mais néanmoins si l'on prend certains types de chacune d'elles, dont les caractères ne sont pas absolument nets, quelqu'un qui ne serait pas bien exercé, les confondrait à peu près sûrement, tout au moins par leur forme extérieure. Il est bon de décrire comme type de l'espèce, dans ce cas, des êtres absolument intacts, c'est à dire, aucunement déformés, ni par pression à l'état vivant ou dans les flacons d'alcool, ou par toute autre cause. On sait, en effet, combien, parfois, ces animaux revêtus d'une enveloppe molle, se laissent déformer et rendre méconnaissables quand ils sont placés vivants et en trop grand nombre dans un flacon d'alcool.

On ne saurait trop recommander aux voyageurs de ne pas tasser ainsi ces êtres mous dans leur flacons, comme ils le font, hélas ! trop souvent, pour gagner un peu de place.

Les mêmes précautions peuvent ne pas être prises quand il s'agit de *Scalpellum*, par exemple, car, du moins en général, les plaques qui recouvrent le capitulum et le pédoncule de ces animaux leur donnent une rigidité suffisante pour éviter à peu près toute déformation.

J'ai rencontré dans cet envoi du British Museum trois espèces nouvelles d'*Alepas*, aux quelles j'ai donné les noms d'*A. Belli*, *A. microstoma*, et *A. indica*.

Elles sont, en général, représentées par des échantillons d'assez grande taille, surtout la dernière qui mesure une longueur totale de sept centimètres.

#### 1. ALEPAS BELLI, nov. sp. (Pl. 24. figs. 1 A, 2, 3, 17, 18, 19, 28, & 29.)

*Diagnose*.—Capitulum à peu près triangulaire, avec bord antérieur presque droit. Pas de crête dorsale véritable, mais légère saillie sur toute la longueur. Orifice externe allongé, rétréci à sa partie supérieure, arrondi, au contraire, à sa partie inférieure.

Pas de scuta.

Cuticule presque lisse, avec, seulement, quelques plis irréguliers. Surface dorsale absolument lisse, délimitée par un sillon.

Pédoncule de forme cylindrique, séparé du capitulum par un léger rétrécissement de celui-ci.

Appendices caudaux avec quinze articles.

Rames internes des 5<sup>e</sup> et 6<sup>e</sup> paires de cirrhes atrophiées et portant, chacune, vingt-sept articles.

*Habitat*.—Côtes de Cuba.



Cette espèce, dédiée au Professeur J. Bell, du British Museum, se rapproche d'*A. Lankesteri*, A. Gruvel.

La forme générale de l'animal est assez gracieuse, un peu élancée et non massive. La longueur du pédoncule est bien proportionnée à celle du capitulum.

Le *capitulum* est à peu près triangulaire, avec son bord antérieur presque droit et son bord dorsal à peu près régulièrement arrondi. Cependant il fait une légère saillie vers son tiers inférieurs et se relève au-dessus de l'orifice du capitulum pour former une saillie assez développée précédée d'une partie légèrement creuse. Il n'y a pas de crête véritable, mais ce bord dorsal fait cependant sur toute sa longueur une légère saillie aplatie.

Les parties latérales du capitulum sont nettement comprimées ce qui donne précisément à l'animal son élégance particulière. La partie la plus large, antéro-postérieure, du capitulum est placée au niveau de l'insertion du muscle adducteur des scuta.

L'orifice externe est de forme allongée, rétréci vers sa partie supérieure, dilaté en rond à sa partie inférieure où viennent se placer les cirrhes. Les lèvres qui le bordent présentent, extérieurement, un bord légèrement déprimé et rempli de plissements parallèles les uns aux autres et tous perpendiculaires au bord antérieur de l'orifice.

La cuticule qui recouvre le capitulum est presque lisse, marquée seulement de quelques plis irréguliers, rares ; mais il existe dans la région dorsale et de chaque côté un sillon assez profond qui délimite une surface allongée, allant de la dépression sus-buccale presque jusqu'à la partie inférieure du capitulum. Cette surface est extrêmement lisse, au contraire du reste de la surface capitulaire, mais elle est sur le même plan que celle-ci—c'est à dire, ni en creux ni en relief par rapport à elle. Le sillon qui la délimite est rectiligne de chaque côté, puis remonte vers la partie dorsale, antérieurement et postérieurement, pour aller rejoindre son symétrique.

La cuticule est épaisse résistante, colorée en jaune tout au moins, après son séjour dans l'alcool, et si peu transparente qu'il est impossible d'apercevoir au travers le corps de l'animal, comme cela a lieu pour *A. Lankesteri*, A. Gruvel, par exemple.

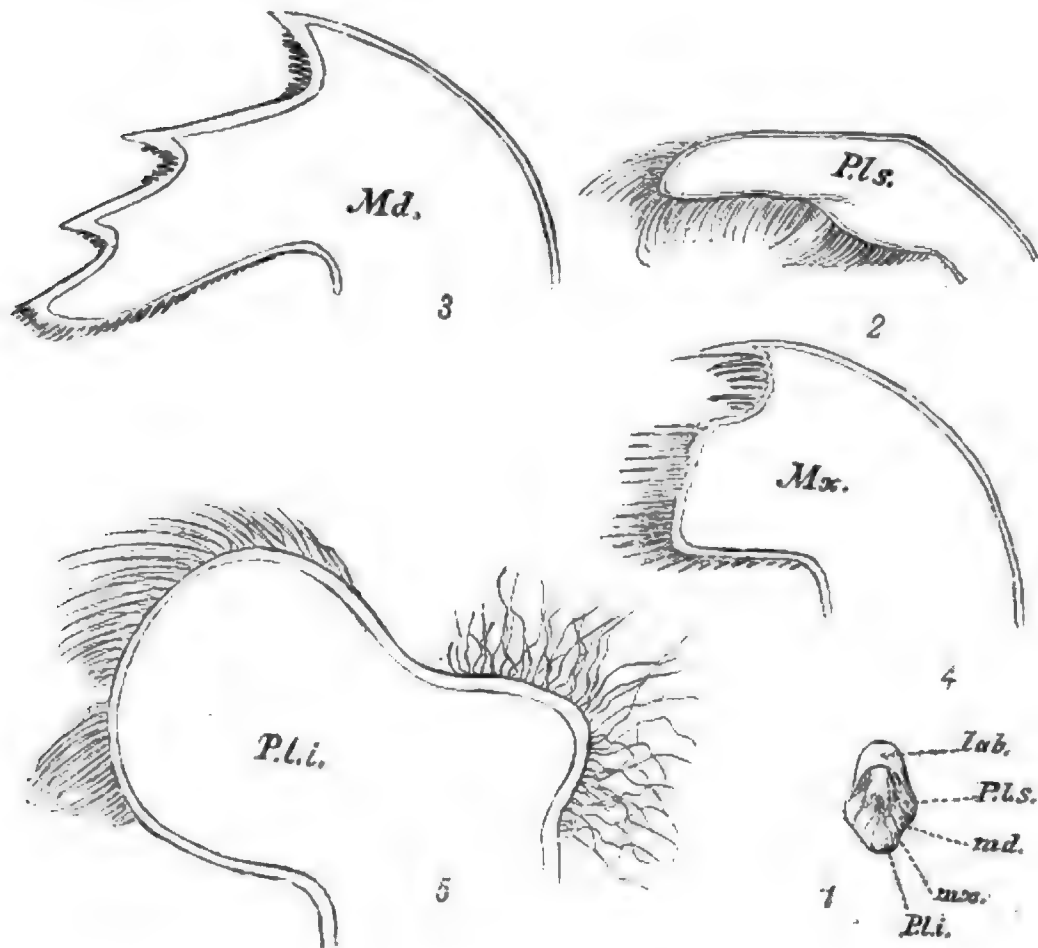
La surface externe de cette cuticule est ornée de granulations chitineuses arrondies dont quelques-unes portent des crochets. Il existe aussi quelques soies sensibles, mais rares cependant.

Les dimensions du capitulum du plus grand échantillon sont :—Longueur, 25 mm. ; largeur, 16 mm.

Le *pédoncule* continue le capitulum dont il est séparé par un léger rétrécissement, sans que, cependant, cette séparation soit bien nette. Il est un peu plus long que le capitulum, mais beaucoup plus étroit, de forme cylindrique, c'est à dire avec une diamètre à peu près le même aussi bien au sommet qu'à la base. La cuticule s'y continue avec les mêmes caractères que sur le pédoncule, mais avec une épaisseur un peu moins forte, cependant, et des sillons parallèles et plus nettement accusés.

Longueur du pédoncule, 32 mm. ; largeur, 9.5 mm.

*Habitat.*—Les échantillons d'*A. Belli* proviennent des côtes de Cuba.  
Collection du British Museum.



*Alepas Belli*, nov. sp.

Fig. 1. Mamelon buccal, vu par la partie supérieure : *Lab.*, lèvre sup. ; *Pl.s.*, palpe labial sup. ;

*md.*, mandibule ; *mx.*, mâchoire ; *Pl.i.*, palpe labial inférieur.

Fig. 2. Palpe labial supérieur droit.

Fig. 3. Mandibule droite.

Fig. 4. Mâchoire droite.

Fig. 5. Palpe labial inférieur droit.

*Appareil buccal.*—Le *labre* fait une forte saillie en avant, sa partie interne est fortement chitinisée, et présente sur son bord libre des nodules chitineux arrondis représentant les dents. Les *palpes* sont allongés, aplatis en rame et couverts de poils sur les bords antérieurs et inférieurs (fig. 2).

Les *mandibules* ressemblent beaucoup à celles d'*A. Lankesteri*, elles sont cependant

plus allongées et plus fortement armées de pointes chitineuses sur les parties latérales des dents. Ces dents sont au nombre des trois, la quatrième formant la pointe inférieure de la pièce (fig. 3).

Les *mâchoires* diffèrent simplement de celles d'*A. Lankesteri*, en ce que la partie inférieure, scalariforme, se termine en saillie à l'angle inférieur qui est arrondi dans l'espèce précédente. L'encoche est aussi un peu moins profonde chez *A. Belli* (fig. 4).

Enfin les *palpes de la lèvre inférieure* constituent les pièces les plus volumineuses. Leur bord libre est nettement arrondi et couvert de deux touffes de soies longues, flexibles, non séparées par une encoche (fig. 5).

*Cirrhes*.—En ce qui concerne les cirrhes, j'ai rencontré dans cette espèce des anomalies nombreuses et tout à fait singulières. L'atrophie des rames est un fait extrêmement commun, et je crois pouvoir dire, d'après les échantillons examinés que cette atrophie se rencontre plus souvent que la disposition normale. Je ne veux pas parler en fait d'irrégularités de l'atrophie qui se manifeste sur la rame interne des 5<sup>e</sup> et 6<sup>e</sup> paires de cirrhes. Celle-ci est, en effet, normale; mais j'ai trouvé des rames atrophiées sur les quatre autres paires—tantôt la rame externe, tantôt l'interne, tantôt d'un côté, tantôt de l'autre. Cette irrégularité absolue indique nettement que c'est là un phénomène accidentel et dont il est impossible de tenir compte dans la spécification. Seuls les caractères *permanents* doivent être signalés. Si j'insiste sur ce point, c'est pour montrer l'inconvénient grave qui peut résulter de l'étude des cirrhes chez un seul individu, et dont le résultat peut-être une erreur de détermination.

1<sup>re</sup> paire (Pl. 24. fig. 28). Les deux rames sont inégales, la rame antérieure étant plus courte que la postérieure d'environ le quart de la longueur de cette dernière. Elles sont épaisses et garnies de très nombreuses soies longues fines et légèrement barbelées sur leur extrémité libre et la moitié de leur longueur.

2<sup>e</sup> paire. Rames à peu près égales, l'externe dépassant cependant légèrement l'interne. Leur longueur est environ la moitié en plus de la rame postérieure de la 1<sup>re</sup> paire. Les articles sont assez allongés et chacun d'eux porte, antérieurement, une seule paire de soies longues, finement barbelées à l'extrémité et à sa base deux paires très courtes, glabres, l'antérieure dépassant un peu la postérieure.

3<sup>e</sup> paire et 4<sup>e</sup> paire à peu près identiques à la deuxième, mais leur longueur est un peu plus considérable.

5<sup>e</sup> paire et 6<sup>e</sup> paire. Les rames externes sont normales et semblables aux deux précédentes, mais les rames internes sont *atrophiées* et égales, chacune d'elle portant 27 articles. Leur longueur atteint seulement environ le tiers de celle de la rame externe. Les soies qu'elles portent sont aussi extrêmement réduites, excepté le dernier article qui porte une touffe de soies plus longues.

*Appendices terminaux* (Caudal appendages).—Ils sont formés de 15 articles seulement, assez larges à la base, avec des soies nulles ou très courtes; les articles s'allongent vers le sommet, ainsi que les soies qui, au nombre de trois ou quatre, couronnent le sommet du dernier article.

*Appendices filamenteux* (Filamentary appendages).—Une seule paire, courte, terminée en pointe effilée et située à la base de la 1<sup>re</sup> paire de cirrhes.

*Pénis*.—Le pénis (Pl. 24. fig. 29) est long (env. 8 mm.). Forme cylindrique, allant en s'effilant régulièrement jusqu'au sommet qui est en pointe mousse.

Annulation nette sur la moitié terminale; quelques rares poils disséminés à la surface et une touffe à son sommet.

*Affinités*.—En remerciements de l'extrême bienveillance avec laquelle M. le Professeur Jeffrey Bell a bien voulu m'accueillir au British Museum pendant mon séjour à Londres, et aussi pour la grande courtoisie qui a toujours régné dans nos rapports réciproques, je lui dédie cette espèce nouvelle. *Alepa Belli* est voisin d'*A. Laukesteri*.

## 2. ALEPAS MICROSTOMA, nov. sp. (Pl. 24. figs. 1 B & B', 7 & 8.)

*Diagnose*.—Forme générale plus globuleuse que celle du précédent. Bord antérieur du capitulum droit au niveau de l'orifice externe, mais saillant et arrondi en dessous.

Orifice externe étroit, cordiforme avec une gouttière dorsale. Le capitulum présente une légère crête tout le long du bord dorsal, surtout développée à la partie inférieure. Toute la surface est striée de sillons profonds, nombreux et irréguliers, excepté une surface courbe dorsale, délimitée par un sillon qui en fait tout le tour.

Pas de scuta. Cuticule plus mince que celle d'*A. Belli*.

Pédoncule à peu près régulièrement cylindrique.

Appendices caudaux formés de 15 articles.

Rames internes des 5<sup>e</sup> et 6<sup>e</sup> paires de cirrhes atrophiées et inégales (29 et 26 articles).

*Habitat*.—Madère.

J'ai appelé cette espèce *A. microstoma* à cause de la petitesse relative de son orifice externe. Voisine de la précédente.

La forme générale de l'animal est plus globuleuse que celle du précédent. Le capitulum au lieu d'être comprimé est plutôt un peu renflé latéralement; sa longueur est moindre et sa largeur plus considérable, ce qui, par rapport à l'ensemble, lui donne un aspect moins élégant et plus trapu que le premier.

La plupart des grands échantillons que j'ai eu entre les moins étaient plus ou moins déformés et les caractères semblaient moins nets que sur un plus petit, absolument intact et que je prendrai par conséquent comme type de cette espèce, au point de vue, tout au moins, de la forme extérieure.

Le bord antérieur du capitulum est droit en face de l'orifice, mais, au-dessous, il fait une saillie arrondie en avant et se rétrécit à sa partie inférieure pour aller se continuer avec le pédoncule. Le bord dorsal, régulièrement arrondi sur toute sa longueur, présente une très petite crête qui s'accentue un peu plus à la partie inférieure.

L'orifice externe, sans être saillant, forme une sorte de tube, nettement séparé de la partie inférieure du capitulum par un sillon transversal. Cet orifice, assez petit, est cordiforme, avec un très petit sillon à sa partie supérieure, qui s'élargit tout à coup très régulièrement pour laisser passer les cirrhes.

Toute la surface du capitulum est striée de sillons profonds, mais très nombreux et irréguliers, excepté une surface dorsale délimitée de chaque côté par un sillon courbe qui, partant du sommet du capitulum, descend d'abord à peu près parallèlement à la ligne dorsale, puis s'en éloigne progressivement, pour venir la rejoindre brusquement à la partie inférieure du capitulum.

La surface courbe ainsi délimitée est absolument lisse et un peu en relief par rapport au reste de la surface capitulaire.

Le capitulum est nettement séparé du pédoncule par un rétrécissement brusque, mais la cuticule se continue à sa surface avec les mêmes caractères.

La cuticule est moins épaisse que chez *A. Belli*, de couleur blanchâtre, sale. Elle porte comme ornements des nodules avec ou sans crochets comme chez *A. Lankesteri*, *A. Gruvel*, ainsi que des soies sensibles assez nombreuses.

Les dimensions du plus grand échantillon sont :—

Longueur du capitulum, 23 mm. ; largeur, 17 mm.

Longueur du pédoncule, 24 mm. ; largeur, 9 mm.

Comme on le voit, le pédoncule est seulement un peu plus long que le capitulum ; il est à peu près régulièrement cylindrique, un peu plus large, cependant, aux deux extrémités qu'au centre.

Le manteau ne présente rien de particulier.

*Habitat*.—Les échantillons étudiés proviennent de Madère.

Collection du British Museum.

*Appareil buccal*.—L'appareil buccal, dans son ensemble, est tellement identique à celui de l'espèce précédente, que je n'aurais, pour ainsi dire, qu'à répéter mot pour mot ce que j'en ai dit. Je le juge inutile.

*Cirrhes*.—Je n'ai pas à répéter ici ce que je disais à propos d'*A. Belli*. Les deux échantillons étudiés présentaient tous deux une constitution normale, l'atrophie portant seulement sur les rames internes des 5<sup>e</sup> et 6<sup>e</sup> paires de cirrhes.

*1<sup>re</sup> paire*. La rame postérieure dépasse l'antérieure de ses 5 ou 6 derniers segments, bien que le nombre des segments soit très différent : 32 à la grande, 17 à la petite, mais cela tient à ce que chez la première ils sont beaucoup plus courts que chez la seconde.

Ces rames sont moins larges que chez *A. Belli* et chaque article au lieu de porter un grand nombre de soies, n'en présente qu'une vingtaine environ, qui sont surtout très courtes sur la rame postérieure, elles sont raides et finement barbelées sur leur moitié libre.

*2<sup>e</sup> paire*. Rames égales, chacune d'elle étant environ  $\frac{1}{3}$  plus longue que la rame postérieure de la 1<sup>re</sup> paire. Elles sont formées par un grand nombre d'articles très courts, portant chacun deux grandes soies longues raides et finement barbelées, deux très courtes en arrière de celles-ci et deux semblables à ces dernières et insérées latéralement.

*3<sup>e</sup> et 4<sup>e</sup> paires*. Un peu plus longues que la deuxième par les rames, dont l'interne est plus courte de deux segments que l'externe. Même disposition des soies.

5<sup>e</sup> paire. Rame interne atrophiée, avec 29 articles, mais les soies sont beaucoup moins réduites que chez *A. Belli*.

6<sup>e</sup> paire. Rame interne également atrophiée, mais formée seulement de 26 articles.

Les rames internes des 5<sup>e</sup> et 6<sup>e</sup> paires sont donc *inégaies*, au contraire d'*A. Belli* où elles sont *égales*.

*Appendices terminaux* (Caudal appendages).—Semblables à ceux de la précédente espèce. Ils présentent également 15 articles, dont le terminal très court, porte un bouquet de soies.

*Appendices filamenteux* (Filamentary appendages).—Une seule paire assez longue à la base de la première paire de cirrhes.

*Pénis*.—Court (env. 6 mm.), trapu, conique, terminé en pointe mousse. Formé d'un grand nombre d'anneaux très courts, avec quelques très rares soies à la surface et un bouquet au sommet.

*Affinités*.—Cette espèce se rapproche beaucoup de la précédente, dont elle diffère cependant par la forme extérieure et un certain nombre de caractères internes que nous avons mis en relief.

Je lui ai donné le nom d'*A. microstoma*, tiré du caractère anatomique de la bouche, très petite par rapport au volume de l'animal.

### 3. ALEPAS INDICA, nov. sp. (Pl. 24. figs. 1 C, 4 & 4', 21 to 27.)

*Diagnose*.—Le corps entier de l'animal semble être tout d'une venue, sans séparation nette entre le capitulum et le pédoncule qui est extraordinairement développé. Le capitulum est très comprimé latéralement, avec le bord antérieur droit et le bord dorsal régulièrement courbe; ce bord porte une crête transparente, haute d'environ 1 millimètre, sur toute sa longueur. L'orifice externe a la forme d'un triangle curviligne sans gouttière dorsale, et bordé de lèvres très nettement frangées. La cuticle est mince, transparente, et ornée de plissements très fins, assez difficilement visibles à l'œil nu.

Le pédoncule fait suite au capitulum sans transition. Sa longueur atteint environ trois fois et demi, et sa largeur égale à peu près celle du capitulum.

Pas de scuta. Appendices caudaux formés de 12 articles. Rames internes des 5<sup>e</sup> et 6<sup>e</sup> paires de cirrhes atrophiées et inégales (25 et 21 articles).

*Habitat*.—Singapour.

A cause de son origine, j'ai appelé cette espèce *A. indica*. Elle vient se placer, quoique très différente, quant à sa forme extérieure, entre *A. cornuta*, Darwin, et *A. microstoma*, A. Gruvel.

Cette troisième espèce est, certainement, une des plus curieuses que je connaisse appartenant à ce genre, à cause de la longueur vraiment hors de proportion de son pédoncule relativement à celle du capitulum.

Bien que les échantillons ne soient pas dans un remarquable état de conservation, il m'a été possible d'en faire l'étude complète.

Le corps tout entier de l'animal semble être tout d'une venue à cause de la longueur du pédoncule. Il est coloré, après séjour dans l'alcool, en marron foncé tirant un

peu sur la teinte lie de vin. La cuticule est presque aussi transparente que celle d'*A. Lankesteri*.

Le *capitulum* est beaucoup plus comprimé latéralement que chez *A. Belli*. Son bord antérieur est droit, le bord dorsal régulièrement courbe, porte une crête transparente, haute de près d'un millimètre, sur toute sa longueur.

Rien ne rappelle la surface dorsale signalée chez les deux autres espèces. La surface toute entière du *capitulum* est lisse, sans stries ni sillons, excepté dans la région de l'orifice.

Celui-ci a la forme d'un triangle curviligne, dont la partie inférieure est occupée par les cirrhes, sans qu'il existe trace, à la partie supérieure, d'une gouttière quelconque, comme dans l'espèce précédente, par exemple. L'orifice est bordé de lèvres très nettement frangées, avec des sillons transversaux très apparents, placés sur les parties latérales. Sans être saillant, l'orifice dépasse légèrement le bord antéro-inférieur du *capitulum*, dont il est séparé par une légère dépression au-dessus de l'insertion du muscle adducteur des scuta.

Le *capitulum* se rétrécit légèrement à sa partie inférieure pour former le pédoncule, mais la limite nette entre les deux est assez difficile à saisir.

La cuticule mince, transparente, est ornée de plissements très fins, assez difficilement visibles à l'œil nu. On trouve à sa surface des plages formées de tubercules chitineux de différentes grosseur, les plus gros étant généralement au centre. On trouve dans quelques-unes de ces plages une soie sensitive, mais de position tout à fait variable. Les plages elles-mêmes sont disposées très irrégulièrement.

Le *pédoncule* qui fait suite au *capitulum* est tout d'une venue. Sa longueur égale environ trois fois et demi celle du *capitulum* et sa largeur est à peine moins considérable. La cuticule qui le recouvre, continuation directe de celle du *capitulum*, est lisse et présente quelques ornements semblables à ceux déjà décrits.

Les dimensions du plus grand échantillon sont :—

Longueur du *capitulum*, 21 mm. ; largeur, 18 mm.

Longueur du pédoncule, 70 mm. ; largeur, 13.5 mm.

*Habitat*.—Ces échantillons proviennent de Singapour, dans l'Inde Anglaise. Offert par J. Russell, 1886.

British Museum Collection.

*Appareil buccal*.—Sauf quelques détails, l'appareil buccal de cette espèce est identique à celui des deux précédentes.

Les dents du *labre* sont de simples eminences irrégulières de la cuticule, n'ayant que vaguement la forme de dents. La partie interne de cette pièce présente des ornements qui sont sur les parties latérales de fortes soies et des formations pectinées robustes (fig. 22) et dans la région moyenne des formations également pectinées, mais beaucoup plus fines.

Les *palpes* sont identiques (Pl. 24. fig. 23). Les *mandibules* portent sur les parties



latérales, en arrière des dents, des formations pectinées très robustes (fig. 24). Les mâchoires et les palpes de la lèvre inférieure ne présentent rien à signaler (Pl. 24. figs. 25 et 26).

*Cirrhés.*—La symétrie de toutes les rames est absolue, dans cette espèce et l'atrophie ne se manifeste également que sur les rames internes des 5<sup>e</sup> et 6<sup>e</sup> paires.

1<sup>re</sup> paire. La rame postérieure dépasse l'antérieure de ses 5 derniers articles. La rame antérieure très large à la base, est couverte d'un grand nombre de soies finement barbelées.

2<sup>e</sup> paire. Les rames, égales en longueur, atteignent environ le double de la longueur de la rame postérieure de la 1<sup>re</sup> paire. Les soies y sont disposées comme dans *A. microstoma*, mais il existe en plus une paire de soies courtes en arrière, et la partie antéro-supérieure des segments est fortement saillante.

3<sup>e</sup> paire. Rames égales, dépassant celles de la 2<sup>e</sup> paire d'environ  $\frac{1}{2}$  de leur longueur.

4<sup>e</sup> paire. Rames égales, dépassant celles de la 3<sup>e</sup> paire d' $\frac{1}{4}$  environ de leur longueur.

5<sup>e</sup> paire. Rame externe normale. Rame interne atrophiée, formée de 25 articles, avec soies atrophiées. Le dernier article couronné par un bouquet de 6 soies.

6<sup>e</sup> paire. Rame externe normale. Rame interne également atrophiée, mais formée de 21 articles seulement.

Les rames internes des 5<sup>e</sup> et 6<sup>e</sup> paires sont donc *atrophiées* et *inégaies* comme chez *A. microstoma*.

C'est là un caractère spécifique, sur lequel je me suis appuyé pour établir le tableau synoptique qui suit. Il est suffisamment précis pour pouvoir être employé dans la classification. Il est à remarquer, en effet, que, lorsque les rames atrophiées ne portent pas le même nombre d'articles, il y a une différence d'au moins 3 ou 4, suffisante, par conséquent, pour pouvoir être facilement contrôlée.

*Appendices terminaux.*—Les appendices terminaux sont seulement formés de 12 segments ; ceux qui sont à la base sont larges et courts, les autres étroits et longs. Les quatre derniers seuls présentent des soies nettes et le dernier, court, se termine par un bouquet de soies.

*Appendices filamenteux.*—Une paire à la base de la 1<sup>re</sup> paire de cirrhe, autant que j'ai pu le voir avec des animaux en aussi mauvais état.

*Pénis.*—Assez long et cylindrique assez peu nettement annelé.

*Affinités.*—Si jamais nom eut été bien porté par un animal, c'eût été celui de *pedunculata*, mais comme il appartient déjà à une espèce de Hoek, je désignerai—tout simplement celui-ci par son lieu d'origine—*A. indica*.

Tableau synoptique des espèces du genre ALEPAS, Sander-Rang.

1. Scuta présents.	Scuta présents mais recou- verts par la cuticulo.	Rames int. des 5 <sup>e</sup> et 6 <sup>e</sup> paires normales.	Orifice très court, à lèvres frangées, très petite espèce, presque toujours fixée sur <i>Cidaris</i> .....	<i>A. minuta</i> , Philippi.
		Rames int. des 5 <sup>e</sup> et 6 <sup>e</sup> paires atrophiquées et inégaux.	Orifice non proéminent, mais nettement tubulaire. Para- sito sur Méduses .....	<i>A. parasita</i> ?, Sander-Rang.
			Forme carrée. Orifice nettement tubulaire .....	<i>A. quadrata</i> , Auriv.
		Rames int. des 5 <sup>e</sup> et 6 <sup>e</sup> paires normales.	Orifice petit, tubulaire, légèr. proéminent. Pas de crêtes dorsales. Pédonculo assez long .....	<i>A. pedunculata</i> , Hock.
2. Pas de scuta.	Rames int. des 5 <sup>e</sup> et 6 <sup>e</sup> paires atrophiquées.		Orifice tubuleux, proéminent et étroit .....	<i>A. tubulosa</i> ?, Quoy et Gaimard.
		Rames atrophiquées égales.	Orifice légèr. proéminent, 3 à 4 crêtes médianes et dorsales, peu développées .....	<i>A. japonica</i> , Auriv.
			Orifice légèr. ouvert, pas de crête médiane, mais bord dorsal légèr. saillant de toute sa longueur .....	<i>A. Belli</i> , A. Gruvel.
			Orifice légèr. saillant, trois crêtes dorsales assez développées, dont une au-dessus de l'orifice.	<i>A. cornuta</i> , Darwin.
			Orifice non saillant, allongé, non tubulaire, une crête saillante sur toute la partie dorsale .....	<i>A. indica</i> , A. Gruvel.
		Rames atrophiquées inégaux.	Orifice étroit, cordiforme, une légère crête générale dorsale, surtout développée à la base .	<i>A. microstoma</i> , A. Gruvel.
			Orifice légèr. tubulaire et sail- lant, une très légèr crête dorsale générale, cuticule ex- trêmement transparente ....	<i>A. Lankesteri</i> , A. Gruvel.

*Famille des Pentaspidés. (PENTASPIDÆ.)**Sous-famille des Lépadinés. (LEPADINÆ.)*II. Genre *PÆCILASMA*, Darwin, 1851.

Ce genre n'est représenté, dans l'envoi qui m'a été fait, que par une seule espèce et même un unique échantillon que, bien entendu, j'ai pris le plus grand soin de ne pas détériorer.

J'estime, en effet, que toutes les fois qu'une espèce est nouvelle, on qu'on la suppose telle pour de nombreuses raisons, il faut, quand elle n'est représentée que par un seul échantillon, se borner à décrire l'extérieur de celui-ci, afin d'en tirer les caractères spécifiques. Mais l'animal doit être conservé intact, comme type qui sera étudié plus complètement s'il arrive qu'un ou plusieurs individus semblables soient trouvés plus tard.

Il se peut cependant, que, dans certains cas, les caractères extérieurs seuls si ont absolument insuffisants pour établir une diagnose précise. Dans ces conditions, l'étude de l'animal lui-même s'impose—mais alors, les plus grandes précautions doivent être prises pour le détériorer le moins possible et un dessin très rigoureux doit être fait avant d'y toucher.

Dans le cas présent, les caractères extérieurs seuls, n'ayant paru suffisants pour justifier la création d'une nouvelle espèce, je n'ai pas cru devoir détériorer le type et je ne donnerai, par conséquent, que la description de l'extérieur.

Cet échantillon a été trouvé par moi, fixé sur le pédoncule de l'un des exemplaires d'*Alepa indica*, A. Gruvel, dont j'ai donné plus haut la description complète.

*PÆCILASMA MINUTA*, nov. sp. (Pl. 24. fig. 5.)

*Diagnose.*—La forme générale du corps est assez élégante et élancée. Le capitulum est comprimé latéralement, surtout dans sa partie supérieure. Terga triangulaires, à apex pointu et saillant. Bord scutal avec une encoche en face de laquelle vient se placer le sommet du segment antérieur du scutum. Cette encoche est suivie d'une dent qui se place entre les deux segments de cette dernière plaque. Scuta très développés, formés par deux segments, un antérieur allongé, un postérieur large.

Carène courte, uniformément étroite, avec une crête dorsale.

Pédoncule à peu près régulièrement cylindrique; atteint environ la moitié de la longueur de capitulum.

## Dimensions :—

Longueur du capitulum, 2.6 mm.; largeur, 1.5 mm.

Longueur du pédoncule, 1.23 mm.; largeur, 0.61 mm.

A cause de ses petites dimensions, j'ai donné à cette espèce nom de *P. minuta*. Elle ne se rapproche nettement d'aucune espèce connue. C'est cependant de *P. lenticula*, Auriv., qu'elle semble être la plus voisine.

Le corps tout entier de cet animal présente une forme assez gracieuse et élégante. Les plaques capitulaires sont minces et permettent d'apercevoir par transparence le

corps de l'animal qu'elles recouvrent. Comme ce corps est coloré en jaune-orangé, cela donne au capitulum une teinte légère. La cuticule qui sépare les plaques est jaunâtre et celle qui recouvre le pédoncule est un peu rouge-brique; ces couleurs étant, bien entendu, celles de l'animal qui a séjourné longtemps dans l'alcool.

Le *capitulum* est comprimé latéralement surtout dans sa partie supérieure. Les pièces qui le recouvrent sont serrées les unes contre les autres et ne laissent aucun espace purement membraneux.

Les *terga* sont triangulaires, à sommet pointu et saillant. L'angle basal est tronqué, le bord basal présente de sa région antérieure une encoche, en face de laquelle vient se placer le segment antérieur du scutum correspondant. Cette encoche est suivie d'une dent qui est exactement en face de la ligne de suture, entre les deux segments de ce même scutum. Le reste du bord est parfaitement droit.

Les *scuta* sont très développés et chacun est divisé en deux segments, un antérieur et un latéral, par une scissure légèrement convexe antérieurement qui va de l'umbo à l'apex.

Le segment antérieur est très saillant en avant. Le maximum étant environ au niveau du tiers supérieur. L'angle supérieur est régulièrement arrondi, l'angle basal très aigu. C'est lui qui porte l'insertion du muscle adducteur des *scuta*.

Le segment latéral est, de beaucoup, le plus développé des deux. Le bord basal droit forme une très légère pointe à son point de contact avec l'angle basal du segment antérieur. Le bord dorsal ou carénal est régulièrement courbe; enfin le bord tergal est absolument droit.

On aperçoit encore, à l'umbo des *terga* et des *scuta*, les plaques embryonnaires. On ne trouve de stries visibles ni sur l'une ni sur l'autre de ces pièces.

La *carène* est courte puisqu'elle dépasse à peine la milieu du bord dorsal du capitulum. Elle est uniformément étroite du sommet à la base, où, cependant, elle s'élargit un peu. Elle présente une crête dorsale nette, mais arrondie.

La base du capitulum se rétrécit beaucoup pour donner insertion au pédoncule qui, aussitôt, se dilate et déborde légèrement les pièces capitulaires formant cette base.

La longueur du pédoncule ne dépasse guère la moitié de celle du capitulum. Il est à peu près régulièrement cylindrique, un peu plus large cependant vers le sommet qu'à la base. La cuticule qui le recouvre, assez mince, jaune-rougeâtre, présente de petites granulations chitineuses un peu plus colorées que le reste de la surface et disposées à peu près régulièrement en séries circulaires et parallèles.

*Affinités.*—En raison de l'extrême petitesse de l'individu unique qui a servi à cette étude, j'ai donné à l'espèce le nom de *P. minuta*. Je ne veux pas dire, bien entendu, que cette espèce est très petite, il est possible qu'elle atteigne même une certaine taille, mais je crois qu'elle ne doit jamais dépasser de beaucoup les dimensions que je viens de donner.

Par sa forme extérieure, cet animal n'est comparable à aucune espèce connue. Celle dont il semble le plus se rapprocher est *P. lenticula*, Aurivillius\*.

\* On trouvera dans mon Mémoire sur les Cirripèdes du 'Travailleur' et du 'Talisman,' le tableau synoptique des espèces du genre *Pacifasma*. —A. G.

*Famille des Polyaspidés. (POLYASPIDÆ.)**Sous-famille des Pollicipinés. (POLLICIPINÆ.)*III. *Genre SCALPELLUM, Leach, 1817.*

Dans le genre *Scalpellum* deux espèces seulement à signaler : l'une qui constitue une espèce nouvelle et que je dédie au savant qui a étudié les Cirrhipèdes du 'Challenger,' le Dr. Hoek, petite espèce, extrêmement curieuse et qui ne rappelle aucune forme actuellement connue ; l'autre, que je crois devoir rattacher à *Sc. sexcornutum*, Pilsbry, bien qu'elle diffère du type décrit par quelques caractères, secondaires, il est vrai.

1. *SCALPELLUM HOEKI*, nov. sp. (Pl. 24. figs. 6, 9 to 16, & 20.)

*Diagnose.*—Capitulum plutôt un peu globuleux, formé de 14 plaques, serrées fortes, à stries très nettement marquées. Bord antérieur à peu près régulièrement courbe, avec cependant un angle à la limite des scuta et des terga et une saillie antérieure de l'umbo des pièces rostro-latérales.

La cuticule qui recouvre les plaques est très mince et glabre.

Carène presque droite à sa partie inférieure, fortement arquée à sa partie supérieure. Umbo voisin de l'apex. Pas d'arêtes latérales. Surface dorsale arrondie. Terga à apex légèrement tourné en arrière. Scuta à apex droit. Plaques infra-latérales allongées, étroites et dont la partie inférieure est fortement recourbée en avant. Umbo à la base. Umbo des pièces caréno-latérales à la base et ne dépassant par le bord externe de la carène. Rostre allongé en forme de triangle curviligne. Pas de sous-carène.

Pédoncule assez long par rapport au capitulum, cylindro-conique, orné de huit séries longitudinales et alternes d'écailles très allongées transversalement, libres, largement séparées les unes des autres, excepté dans la région capitulaire ; chaque série porte 8 ou 9 écailles.

*Capitulum.*—Plutôt légèrement globuleux, surtout dans sa région inférieure. Bord antérieur, à peu près régulièrement courbe, mais formant un angle entre les terga et les scuta et une saillie de l'umbo des plaques rostro-latérales. La largeur égale à peu près les  $\frac{2}{3}$  de sa hauteur. Il est formé de 14 plaques fortes, solides, serrées les unes contre les autres, à stries très nettement marquées, recouvertes d'une cuticule absolument lisse. Le bord basal est très légèrement concave et un peu incliné de haut en bas et d'avant en arrière.

*Scutum.*—Forme presque trapézoïde. Bord antérieur régulièrement courbe ; apex à peu près droit à peine rentrant. Bord tergal très légèrement concave, bord supra-latéral droit à peu près égal au précédent. Bord basal convexe et un peu plus long. Une arête plate et un peu large unit l'apex à l'angle latéro-basal ; la plaque porte des stries parallèles non saillantes, qui se continuent sur le reste de la surface.

*Tergum.*—Irrégulièrement triangulaire, car le côté basal est cassé en deux parties faisant entre elles un angle très ouvert. Le bord antérieur est régulièrement et assez fortement courbe ; l'apex tourné en arrière, le bord carénal presque droit. Une arête peu marquée unit l'apex à l'angle basal.

*Carène.*—Étroite au sommet, elle s'élargit rapidement jusqu'à la base où elle est très large et se termine en pointe mousse qui s'avance entre les pièces caréno-latérales jusqu'au niveau du pédoncule. La partie dorsale est arrondie, légèrement carénée et la plaque ne présente pas trace d'arêtes latérales. L'umbo est très voisin de l'apex. Dans sa partie supérieure, cette plaque est fortement recourbée en avant, tandis qu'elle est presque droite dans sa région moyenne et inférieure. Enfin, entre le bord antérieur arrondi et le bord carénal des terga se trouve une petite surface parfaitement calcifiée et qui se trouve dans un plan inférieur, plus profond par rapport au reste de la plaque.

*Plaques supra-latérales.*—Triangulaires, avec le bord tergal et le bord scutal droits et le bord caréno-basal irrégulièrement convexe. Cette plaque porte une arête plate longeant le bord scutal très fortement marquée de stries parallèles qui se poursuivent sur toute la surface. L'umbo est à l'apex qui est droit et en pointe mousse.

*Plaques rostro-latérales.*—Irrégulièrement quadrangulaires, avec le bord scutal presque droit, un peu concave et très obliquement dirigé de haut en bas et d'arrière en avant. Le bord rostral très court est concave, de sorte qu'entre les deux vient se placer le rostre.

Le bord basal, court, est droit et se continue par le bord latéral très convexe s'appuyant sur la plaque infra-latérale. Une arête par de l'umbo et va rejoindre l'angle latéro-basal, délimitant une large surface latérale et une petite surface antérieure triangulaire.

*Rostre.*—Le rostre est très facilement visible à la surface. Il a la forme d'un triangle curviligne allongé. Ses côtés sont légèrement recouverts par le bord rostral des plaques rostro-latérales.

*Plaques infra-latérales.*—Très caractéristiques, un peu en forme de corne d'abondance. La partie supérieure est la plus large et la plaque se rétrécit progressivement jusqu'à son umbo qui est tout à fait à la base. La plaque, allongée à sa partie inférieure, est fortement recourbée en avant. Elle est marquée de stries parallèles très nettes.

*Plaques caréno-latérales.*—Presque la forme d'un triangle rectangle si le côté infra-latéral était droit, mais il est concave en avant. Le bord carénal est à peu près droit et tourne autour de la base de la carène en se dirigeant vers la région médiane et dorsale du pédoncule où il rejoint celui du côté opposé. Une arête plate, large au sommet, étroite à la base, va de l'apex à la base en bordant le côté carénal de la plaque. Cette arête présente des lignes parallèles très nettes qui se continuent sur la plaque et viennent aboutir au bord basal, où elles forment une sorte de dentelure.

Longueur du capitulum, 5.50 mm. ; largeur, 3 mm.

*Pédoncule.*—Le pédoncule est assez long, de forme cylindro-conique. Il est orné de 8 séries longitudinales et alternes de plaques très allongées transversalement, serrées dans la région capitulaire, mais partout ailleurs largement séparées par un intervalle purement chitineux ; leur bord libre présente une saillie médiane dirigée vers la partie inférieure. La cuticule ne les recouvre que vers la base. Chaque série présente 8 ou 9 écailles à peu près semblables.

Longueur du pédoncule, 2.75 mm. ; largeur, 1.75 mm.

*Habitat.*—Océan Pacifique, sans autre indication. Cinq échantillons fixés sur des Bryozoaires.



*Observations et Affinités.*—Cette espèce ne ressemble à aucune des espèces actuellement connues, par la forme de ses plaques infra-latérales et caréno-latérales. Mais par ses autres caractères elle vient se placer à côté de *Sc. luridum*, Auriv., dont elle se distingue, du reste, très facilement, d'après les caractères des pièces que je viens de signaler.

*Etude de l'animal proprement dit.*—Labre allongé triangulaire, encadrant dans ses deux branches latérales, toutes les autres pièces buccales. Son bord libre porte une trentaine de masses chitineuses arrondies, petites, toutes semblables.

Les *Palpes* qui s'attachent en arrière et en dedans sont allongés, triangulaires, avec un bouquet de soies terminales un peu longues et quelques soies dorsales très petites (fig. 13).

Les *Mandibules* portent trois dents fortes avec l'angle inférieur armé de trois pointes chitineuses fortes et sur les parties latérales, de soies courtes et robustes (Pl. 24. fig. 15).

Les *Mâchoires* portent sur leur bord libre une encoche peu profonde située un peu plus du côté dorsal que du côté ventral. La zone dorsale porte deux dents longues et fortes suivies de deux autres rangées plus courtes et moins robustes. Quant à la zone inférieure les dents assez fortes semblent divisées en deux groupes, très peu séparés du reste. Les parties latérales présentent des soies courtes et assez fortes (fig. 14).

Les *Palpes* de la lèvre inférieure sont aplatis, larges, avec un bouquet de grandes soies non barbelées à la pointe antérieure et d'autres sur le bord dorsal et sur le bord libre, mais ici en moins grande abondance. Il y en a aussi sur les parties latérales.

*Cirrhes.*—Les cirrhes sans être très longs, le sont cependant suffisamment et ils sont également, grêles.

La 1<sup>re</sup> paire est assez éloignée de la 2<sup>e</sup>. Les rames sont à peu près égales, l'antérieure, étant cependant un peu plus courte que la postérieure qui semble formée de 8 articles, mais les limites des deux articles basilaires sont peu nettes. Ces articles sont très peu saillants, armés de soies nombreuses, assez courtes et très finement barbelées.

La 2<sup>e</sup> paire a les rames égales et atteignant environ 2 fois la longueur de celles de la première. Chacune d'elles est formée de 10 articles, étroits, allongés, légèrement saillants en avant et portant, en moyenne, 6 séries doubles de soies longues, surtout vers la limite supérieure des articles et finement barbelées.

Les autres paires de cirrhes sont à peu près semblables à la 2<sup>e</sup>, mais un peu plus longues.

*Appendices terminaux.*—Ces appendices sont formés de trois articles nets; l'article basal, le plus long, porte bien vers son milieu une sorte de ligne d'articulation, mais elle ne comprend pas toute la largeur de l'article et ne forme pas, par conséquent, deux segments distincts. Chacun de ces trois articles porte des soies plus longues vers la limite supérieure des articles. Le segment terminal porte un bouquet de longues soies non barbelées et d'autres plus courtes à la base.

Au milieu de chaque article se trouve une soie; deux sur l'article basal.

*Pénis.*—Absent. Pas trace de testicules. J'ai trouvé au-dessous du prosoma une vingtaine d'œufs gros, ovoïdes, et en voie de développement.



Sur les cinq échantillons examinés, trois portaient 2 mâles complémentaires un sur chaque côté, profondément enfoncés dans la cavité interpalléale, 2 n'en portaient qu'un, mais comme on le voit, il y en avait sur tous.

Comme une étude complète de ces petits êtres sera publiée dans les Résultats des Expéditions du 'Talisman' et du 'Travailleur,' la description du mâle de cette espèce y trouvera sa place, qui me semble beaucoup mieux justifiée dans un travail d'ensemble, que dans une description isolée qui ne signifie pas grand'chose.

## 2. SCALPELLUM SEXCORNU, Pilsbry.

L'unique échantillon que j'ai sous les yeux a été désigné par Miers sous le nom de *Sc. verticillatum*, c'est du reste celui que porte encore l'étiquette du flacon qui le renferme. Comme Miers n'a jamais donné ni diagnose, ni description d'aucune sorte pour cette espèce, elle a été de nouveau nommée par Pilsbry en 1897\*.

Je me bornerai, par conséquent, tout simplement, à montrer les quelques points qui ne me semblent par répondre exactement à la description ou à la figure de Pilsbry, mais qui, à mon avis, ne justifient par la création d'une espèce nouvelle. Il est bon, je crois, cependant, d'indiquer ces particularités pour montrer les modifications de détails qui peuvent se rencontrer dans cette espèce.

Forme générale du capitulum triangulaire, le côté rostral presque droit, le côté dorsal convexe. 13 plaques parfaitement calcifiées. Ces plaques, surtout celles de la rangée inférieure, sont séparées par un espace purement chitineux, parfois considérable. La cuticule qui les recouvre en grande partie est couverte de poils fins et courts surtout dans les régions dorsale et ventrale.

*Carène* régulièrement courbe, mais redressée, umbo très rapproché de l'apex. Sa surface dorsale est arrondie, sans trace d'arêtes latérales et nettement carénée; très étroite au sommet, elle s'élargit progressivement vers la base.

*Tergum* triangulaire avec les côtés à peu près droits, le côté carénal étant le plus long et légèrement convexe. Une légère saillie de la plaque va de l'apex, droit et pointu, à l'angle basal. Stries d'accroissement assez nettes, en partie cachées par la cuticule.

*Scutum* convexe, triangulaire, avec le bord ocluseur légèrement concave et le bord tergal droit, mais le bord basal fortement convexe, en partie caché sans la cuticule. Apex pointu et droit. Stries radiales non marquées, les stries d'accroissement seules visibles. Une bordure finement chitineuse et couverte de poils courts, ayant environ 1 mm. dans sa largeur maximum va de l'apex du tergum un peu au-dessous du milieu du bord ocluseur du scutum.

Les plaques *supra-latérales* en forme de triangle curviligne. Umbo à l'apex, en pointe mousse, légèrement recourbée en avant. Bord tergal à peu près droit, bord scutal fortement concave égalant environ 2 fois la longueur du bord tergal, enfin, bord basal fortement convexe et égalant à peu près trois fois la longueur du bord tergal.

*Rostre* triangulaire, dont la largeur égale, au moins, la hauteur. Apex tourné en haut

\* Pilsbry, H. A. "Description of a remarkable Japanese Cirriped (*Scalpellum sexcornutum*).” *American Naturalist*, xxxi, p. 723 (1897).

et légèrement saillant. Toute la partie inférieure de la plaque est recouverte par la cuticule.

Les *plaques rostro-latérales, caréno-latérales* et *subcarénales*, au lieu de se recourber en bas comme dans la description de Pilsbry, ont leur apex dirigé, au contraire, vers le haut et éloigné du capitulum, ce qui les fait saillir considérablement en dehors. Toutes ces plaques sont triangulaires, plus hautes que larges et recouvertes en grande partie par la cuticule.

Pas de plaque *infra-médio-latérales* ni de sous-carène.

Longueur du capitulum, 16 mm. ; largeur, 9 mm.

*Pédoncule*.—Cylindro-conique, aussi large que le capitulum à sa partie supérieure et allant en diminuant progressivement. Quelques rangées circulaires, à peu près parallèles, d'écaillés allongées en forme de pointes et presque cachées par la cuticule couverte de poils très courts et très fins.

Longueur du pédoncule, 10 mm. ; largeur moyenne, 6 mm.

*Habitat*.—Une seul exemplaire recueilli par 22 brasses de fond et par 31° 31' lat. N. et 133° 41' long. E. Inland Sea. Présenté par le Dr. J. G. Jeffreys.

*Observations et Affinités*.—Cette espèce me semble aussi rapprochée de *Sc. Peroni*, Gray, et de *Sc. Scorpio*, Auriv., que de *Sc. villosum*, Leach, ou *Sc. trispinosum*, Hoek, car si la carène est presque droite, comme dans ces dernières espèces, il n'en est pas moins vrai qu'elle est recourbée en avant et qu'il existe une surface antéro-supérieure, en partie cachée par la cuticule, mais qui fait que l'umbo au lieu d'être exactement à l'apex se trouve un peu en arrière de lui\*.

## EXPLICATION DE LA PLANCHE 24.

Fig. 1. Reproduction photographique de :

A. *Alepas Belli*, n. sp.

B et B'. *Alepas microstoma*, n. sp.

C. *Alepas indica*, n. sp.

2. *Alepas Belli*, dessiné d'après nature.

3. Le même, orifice externe du capitulum, vu de face.

4. *Alepas indica*, d'après nature.

4'. Le même. Orifice externe du capitulum, vu de face.

5. *Pæcilasma minuta*, n. sp., d'après nature.

6. *Scalpellum Hoeki*, n. sp.

7. *Alepas microstoma* jeune.

8. Le même. Orifice externe du capitulum, vu de face.

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\* Même remarque que dans la note (\*), p. 289.

Fig. 9. *Scalpellum Hoeki*. Carène et plaques caréno-latérales, vues par la face dorsale.

10. „ Rostre, vu de face.
11. „ Ecailles pédonculaires.
12. „ Mamelon buccal, vu par la partie supérieure.
13. „ Palpe de la lèvre supérieure.
14. „ Mâchoire gauche.
15. „ Mandibule droite.
16. „ Palpe de la lèvre inférieure droit.
17. *Alepus Belli*. Ornaments de la cuticule.
18. „ „ „
19. „ „ „
20. *Scalpellum Hoeki*. Appendices caudaux (caudal appendages).
21. *Alepus indica*. Dents chitineuses du bord supérieur du labre.
- 22 *a* et *b*. Ornaments des parties latérales du labre ; *c*, ornaments de la région moyenne ; *d*, ornaments de la cuticule capitulaire, avec les tubercules et la soie sensitive.
23. Le même. Palpe de la lèvre supérieure.
24. „ Mandibule gauche.
25. „ Mâchoire droite.
26. „ Palpe de la lèvre inférieure, droite.
27. „ Portion de rame de la deuxième paire de cirrhes.
28. *Alepus Belli*. Une soie antérieure de la 1<sup>re</sup> paire de cirrhes.
29. „ Pénis.



IX. *On the Actinian Bunodeopsis globulifera, Verrill.* By J. E. DUERDEN, Ph.D., A.R.C.Sc.(Lond.), Bruce Fellow, Johns Hopkins University. (Communicated by Prof. G. B. Howes, F.R.S., Sec. Linn. Soc.)

(Plates 25 & 26.)

Read 20th February, 1902.

IN a preliminary paper on the Jamaica Actiniaria (1898) I briefly described a new West Indian *Bunodeopsis*, without assigning it any specific name. The year previous I had given a fuller account of two other species of the same genus, and it was intended to institute a comparison with these. In 1899, Prof. A. E. Verrill figured, without any comment in the text, a Bermudas Anemone which he identified as the *Viatrix globulifera* of Duchassaing and Michelotti (1860). Upon the appearance of the paper I drew Prof. Verrill's attention to the similarity between his drawing and the new *Bunodeopsis* which I had obtained, and the year following appeared his description of the form as a new species, *Bunodeopsis globulifera*. The description is limited, however, to an account of the external characters, and gives no attention to the peculiarities of anatomy and minute structure.

A study of the internal structure and histology of the two species of *Bunodeopsis* in 1897 had revealed the presence of a well-developed ectodermal muscle and nerve-layer on the column-wall, along with several other exceptional features, whose significance was not then realized. About this time Dr. Oskar Carlgren (1893, 1900) was directing attention to the importance in Actinian phylogeny of the occurrence of an ectodermal columnar musculature, and its usual association with the absence of gonidial grooves in the stomodæum, absence of ciliated bands from the mesenterial filaments, the non-development of the basilar muscles, and the occurrence generally of a weak internal musculature. Every species of *Bunodeopsis* thus becomes of special interest in connection with this latest phase of the morphological study of the Actinians.

The genus *Bunodeopsis* has been thus defined by me (1897, p. 6):—"Tissues very delicate. Tentacles elongate, readily retractile. Column short, beset proximally with pedunculate or sessile vesicles, the vesicular area much broader than the capitulum. Sphincter muscle feebly developed. More than six pairs of perfect mesenteries."

The genus at present is included within the family Aliciidae, which in the same paper (p. 2) is characterized as follows:—"Hexactinæ with a large, flat, contractile base. Tentacles simple, subulate, and entacmæous. Column with simple or compound outgrowths or vesicles over more or less of its surface, arranged mostly in vertical rows. No cinclides. Sphincter muscle endodermal and diffuse, variable in amount of development. Perfect mesenteries few or numerous. No acontia." In addition to

*Bunodeopsis*, the family contains the genera *Alicia*, *Cystiactis*, and *Thaumactis*, and in 1898 Carlgren included the genus *Phymactis* of Milne-Edwards and Haime.

As a result of the discovery of the ectodermal columnar musculature in *Bunodeopsis*, and also in *Thaumactis*, Carlgren (1898, p. 17; 1900, p. 28) considers that the family Aliciidae as at present constituted is made up of heterogeneous members, and indicates that it will be necessary to remove the two genera mentioned and associate them with the Tribe Protanthæ. He further states that he is preparing a revision of the family. With the many representatives at his command Carlgren is in a much better position for carrying out such a revision than any other student of the Actiniæ, and it is desirable that a fuller account of Verrill's species of *Bunodeopsis* should be available.

#### BUNODEOPSIS GLOBULIFERA, Verrill.

*Bunodeopsis*, n. sp., Duerden, 1898, p. 456.

*Viatritz globulifera*, Verrill, 1899, p. 146, fig. 20.

*Bunodeopsis globulifera*, Verrill, 1900, p. 559, pl. 67, fig. 4.

The base is loosely adherent or free, broad, flattened or encircling marine plants, approximately circular, and thin-walled. In preserved specimens it is usually irregular in form, the middle deeply concave, and the periphery irregularly sinuate; concentric and radiating grooves are also present.

The column is erect, thin-walled, partly transparent, contractile, broad below and gradually narrowing above, passing directly into the tentacles. The limbus is circular in living, but strongly crenulated and lobed in preserved specimens. The lower region of the column, for about two-thirds of the total height, is nearly covered with small spheroidal vesicles, the upper one-third is naked and smooth. The naked region is much more limited in extent in preserved polyps than in living specimens, and Verrill's drawings and description would seem to have been founded upon the former. The apex of the column is devoid of acrorhagi. It is very rarely infolded, but where this takes place the disc, tentacles, and naked part of the column become hidden, and only the region bearing the vesicles remains exposed.

The disposition of the vesicles sometimes appears irregular, though as a rule they are seen to be arranged in vertical rows of different heights, but no regularity in longer and shorter cycles has been established. Towards the base two or three rows of minute tubercles may alternate with a row of large outgrowths. In both his figures Verrill represents the vesicles as irregularly distributed, with scarcely any variation in size, though in the text he notes that larger and smaller ones are mingled together. The species undoubtedly varies greatly in its outward appearance.

The evaginations are simple, sessile or sub-pedunculate, hollow, smooth throughout, opaque, and thick-walled in comparison with the column-wall generally. They are variable in size, some appearing as mere rounded tubercles, while others are seen as distinct vesicular outgrowths; most are spheroidal, but the larger examples may be reniform. Different sizes are intermingled, but in general the organs increase in size from below upwards, at the same time diminishing in numbers.

The tentacles are marginate, strongly entacmæous, and very variable in number and size. Any number from twelve to forty-eight may be present, according to the size of the polyp. Verrill records examples with 18, 20, 22, 24, and 26 tentacles. Three or four cycles are represented, but no regular arrangement, hexameral or otherwise, has been made out. The inner members are mostly very long and slender, tapering towards the extremity, and are smooth, very delicate, and transparent, and sometimes appear minutely spotted. Very often the tentacles are imperfectly developed at some particular region of the periphery, several appearing much shorter than the others, or represented only by mere papillæ. As a rule one such imperfect area will occur, but there may be two, separated by one or more fully developed tentacles (Pl. 25. fig. 1 *b*).

The tentacles are generally overhanging in living polyps, and in preserved specimens they remain nearly erect and tapering, and a little shortened. On one or two occasions they have been found completely infolded, with nothing but the vesicular part of the column showing. Though such a strongly infolded condition is rather exceptional in the present species it is very frequent in *B. antilliensis*, Duerd., and is somewhat remarkable considering the practical absence of a sphincter muscle on the column (p. 302). So complete is the infolding that the tentacles may even pass into the mesenterial chambers, as shown in fig. 11. A basal constriction often occurs at the origin of the tentacle from the disc (fig. 1 *c*), and occasionally a tentacle has become detached, its former position at the margin of the disc being indicated by a circular aperture. The tentacles are thickest just above the basal constriction.

The disc is smooth, circular, flat or slightly convex, and transparent the mesenteries and stomodæum showing through in the living condition. The central part as a rule is elevated in preserved polyps. The mouth is slit-like in living polyps, but in preserved specimens it is widely open and circular, and the lips are thickened and protruding. The stomodæal walls are smooth, and no gonidial grooves are distinguishable.

The polypal wall throughout is nearly transparent and only slightly coloured. During partial contraction the lower part of the column is sometimes a bright, opaque, yellowish green, with brown or black lines or spots. On full distention, the vesicles and column are a clear, delicate, yellowish brown, due to the yellow cells within the endoderm. The tips of the larger vesicles may be a little darker than the rest of the wall, probably owing to the greater concentration of the stinging-cells (fig. 5).

The diameter of the base of the largest specimens is 1.2 cm.; the height varies from 0.5 cm. to 1.3 cm. The length of the inner tentacles is about 1 cm., or nearly the same as the height of the column.

The polyps are essentially shallow-water forms, being usually met with around Jamaica at a depth of three or four feet, with their base encircling the long, narrow, cylindrical stems of the marine weed *Ruppia*, or more rarely adherent to the flattened fronds of *Dictyota* and leaves of *Thalassia*. It occurs in some abundance at Port Antonio, and I have also found it around Kingston Harbour. In this latter area the closely allied *B. antilliensis* is very abundant, but I have not met with it at the former locality.



The polyps are easily detached from the marine plants to which they are adherent ; indeed, in transferring the leaves from the sea, or from one jar to another, the polyps will often slide off. It is doubtful if an actual adherence really takes place, any more than in the case of such organisms as Nudibranchs and Turbellarians. The presence of a basal ciliation, to be described below, would indicate that the contact with foreign bodies is not very close. The extremely weak parieto-basilar muscles and absence of basilar muscles are no doubt the structural features correlated with the incapacity for firm fixation. In the laboratory specimens often free themselves, and, suspended in the water with the tentacles fully expanded, may move slowly around, gradually coming to rest against the sides of the vessel. Probably their movements are assisted by the strong ciliation on the base and column-wall. I have never observed any decided rhythmic movements in swimming. When free the base may be upwards, with the tentacles hanging gracefully downwards; or it may be in its normal lower position, the tentacles then directed upwards and partly overhanging.

Carlgren (1900) also mentions that the *Boloceroidea* *McMurrichi*, obtained by Dr. Stuhlmann from Zanzibar, was likewise found to be able to detach itself and carry on swimming movements much like a Medusa. Like *Bunodeopsis*, the genus *Boloceroidea* is considered to belong to the primitive Protanthææ, as is also *Gonactinia*, another form capable of swimming. Probably such loosely adherent Actinians should be regarded as in some ways intermediate between the free Anemones with a rounded aboral extremity and forms with a flattened firmly adherent base.

#### ANATOMY AND HISTOLOGY.

##### *Base.*

The base is thin-walled, all the three constituent layers being very narrow (Pl. 25. fig. 2). In sections it is usually .03 mm. across. The ectoderm is remarkable for the short, coarse cilia with which it is covered, and which are recognizable in basal sections even when unpreserved in other parts of the polyp. In most preserved polyps only traces of the external ciliation on other parts of the body-wall persist, while the ectodermal stomodæal ciliation is usually very obvious, and less so that of the mesenterial filaments and of the endoderm of the cœlomic cavity. Probably the basal ciliation assists in the movements of the polyps over the leaves of the marine plants on which they settle; or it may help the polyp when it assumes the floating habit. Its presence is incompatible with any firm adherence of the polyps by their base.

The basal ectoderm is constituted mainly of supporting cells, narrow granular gland-cells, and a few clear gland-cells. A small nematocyst, measuring .012 mm., occurs very sparingly. A rudimentary musculature and nerve-layer probably occur, but their presence could not be determined with absolute certainty.

The mesogloea is narrow, and contains a few minute connective-tissue cells. Elsewhere throughout the polyp the mesogloea preserves the same character, that of a narrow, homogeneous layer, containing but a few connective-tissue cells.

The basal endoderm varies much in thickness in different places. Where very narrow,

the cell-contents stain deeply, being highly protoplasmic, and Zooxanthellæ are absent or nearly so; where the layer is broader the cells are more vacuolated, the free surface is somewhat irregular, and the symbiotic algæ are found in large numbers. Throughout the endoderm of the polyp similar broad and narrow areas are represented, according as Zooxanthellæ occur in abundance or are practically absent. A weak circular endodermal musculature can be detected on the base, and in some specimens a nerve-layer separated from the muscle-band by a fibrillar layer. The latter, however, was not recognizable in the section from which fig. 2 was taken.

#### *Column-wall.*

The proximal and distal regions of the column-wall vary somewhat in structure. The former is broad and irregular in outline, owing to the occurrence of the evaginations, while the naked area is very thin and delicate, measuring in sections only .03 mm. across (fig. 4).

The ectoderm of the column-wall is weakly ciliated throughout, and both transverse and vertical sections of the upper part often exhibit fine ridges and grooves as a result of unequal shrinkage (fig. 3). These appearances, however, are more characteristic of the tentacular ectoderm, as shown in the same figure. The constituents are mainly supporting cells and clear gland-cells; nematocysts occur very sparingly, except in the evaginations of which they are very essential elements. A layer of delicate ectodermal muscle-fibres occurs throughout the extent of the column, and in some places the mesogloea is very slightly plaited for its support. The muscle-fibres are arranged with the long axis vertically, so that they are cut cross-ways in transverse sections of the polyp, and constitute a delicate but clearly-marked layer, the fibrils being highly refractive. Outside the band of muscle-fibres occurs a weak nerve-layer (*url*), the two distinctly separated by a narrow interval crossed by fine fibrillar strands (figs. 3, 5, 16).

The nature of the fine strands occurring between the band of muscle-fibres and the nerve-layer, and continued in some cases beyond the latter, is not readily determined. They occur practically throughout the polyp, on both the ectodermal and endodermal surfaces, but are much more definite in some individuals than in others. McMurrich (1890, p. 143) refers to a somewhat similar appearance in various parts of the body-wall of *Cerianthus americanus*, and regards the processes as mesogloæal prolongations. Carlgren (1893, p. 26) describes a nearly similar structure in *Protanthea simplex*, and also considers it to be due to very fine continuations of the mesogloea, which here and there bear strongly refractive bodies, resembling sections of muscle-fibrils. In Carlgren's preparations the details vary greatly according to the manner of preservation of the specimens, and McMurrich's two specimens of *Cerianthus* likewise differed.

The specimens now under consideration were preserved in formol and then transferred to alcohol, and the interval between the mesogloea and the ganglion layer varies greatly in width in different polyps, and even in different regions of the same individual. Usually it is more pronounced on the endodermal side than on the ectodermal, and on

the former the strands sometimes appear slightly reticular in character. Small nuclei occur among the fibrils, and are regarded as the nuclei of ganglion-cells.

The same fibrillar layer is still better developed in some polyps of *B. antillicensis*. It may occur on both the ectodermal and endodermal faces of the mesogloea, and what seem to be the continuations among the ectodermal cells are clearly seen (1891, pl. i. figs. 3, 4). In *Protanthea*, Carlgren (1893, pl. iii. figs. 4, 5) represents the mesogloéal continuations, both on the ectodermal and endodermal aspects, as constituting a nearly compact zone, while in the preparations of *Bunodeopsis* they appear as very distinct coarser strands, rather widely separated one from another.

The nerve-layer in *Bunodeopsis* is, as a rule, very narrow in sections, and appears made up of interlacing fibrils, some seen longitudinally and others in section. In Carlgren's figures of *Protanthea* the layer is represented by minute dots only, indicating the cut ends of the fibrils. Such an appearance also occurs in the stomodæal ectoderm of *Bunodeopsis* (fig. 7, *nr.l.*).

The mesogloea of the column-wall is thin throughout, and both its inner and outer surfaces are smooth, or very slightly plaited to afford additional support for the ectodermal and endodermal musculatures.

The endoderm is broad in the lower region of the polyp, where, as a rule, the cells contain many Zooxanthellæ; but the layer becomes very narrow above, as the symbiotic algæ are either absent or very rare, and the cells are then more charged with protoplasmic contents. The endodermal free surface is everywhere feebly ciliated.

The circular endodermal muscle occurs throughout the column-wall, usually supported on very delicate mesogloéal plaitings. A slight increased development takes place towards the upper extremity, but never to such a degree as to give rise to what may be regarded as a sphincter muscle (fig. 3, *end.m.*). A nerve-layer is usually seen, situated at some distance from the mesogloea, and a little better developed than in the ectoderm.

The evaginations (figs. 4 & 5, *ev.*) are simple, hollow, rounded outgrowths of the lower part of the column-wall, and in transverse sections are seen to be both entocœlic and exocœlic in position, though without any regular alternation. In sections the walls at their thickest are about .065 mm. across. The cavity communicates by a large aperture with that of the cœlenteron. Both the ectoderm and endoderm have undergone certain histological modifications compared with the character of the layers in the column-wall generally. The ectoderm (fig. 5) is broad, somewhat strongly ciliated, and a very distinct zone of oval nuclei occurs just within the outer margin, while smaller, rounded nuclei occur here and there throughout the thickness of the layer. The characteristic elements, however, are the large, thick-walled nematocysts (*nem.*), which occur in some abundance in the outer area of the evaginations. Seen in sections, the nematocysts exhibit few or no structural details, but appear as smooth-walled, nearly homogeneous bodies, irregularly distributed among the supporting cells. The deeper examples more especially are arranged at varying angles with the surface of the ectoderm, but the outer are practically parallel with the supporting cells. The former are probably individuals in process of development and are strongly curved, while when they assume their

mature position at right angles with the surface, they are nearly straight. In macerations the nematocysts appear as represented in fig. 8 *b*. They possess a thickened wall, and exhibit a tubular appearance within, representing the thickened basal part of the thread, but no trace of the finer portion of the thread can, as a rule, be made out.

The musculature and nerve-layer (fig. 5, *nr.l.*) on both sides of the mesoglœa are extremely delicate in the evaginations, but can be clearly recognized in favourable sections. The endoderm is broader than that of the column-wall generally, and is more strongly ciliated. Its cells are usually crowded with Zooxanthellæ (*zoox.*), though in some cases the algæ are very sparse or altogether wanting. The histological character, as a whole, would indicate that the columnar evaginations are to be regarded as special nematocyst-bearing organs.

The size, character, and distribution of the nematocysts possess a certain importance in systematic studies of the Anthozoa, and may be fittingly referred to here as represented throughout the different tissues of the present species.

Carlgren (1900, p. 3) believes that the nematocysts may be made of great assistance in the identification of species of Actiniæ, and even in the recognition of genera. For the time being he roughly divides them into "thin-walled nematocysts," in which the internal spiral thread shows distinctly, and "thick-walled nematocysts," which appear quite smooth. Very often the internal spiral thread is not seen within the latter, while in others it may be recognized, but not so clearly as in the thin-walled form. With regard to their general distribution in the polyp, Carlgren finds the thin-walled variety to occur mostly in the tentacles and disc, but in certain species and genera in the column-wall and stomodæum also. The thick-walled forms are found in all parts of the ectoderm of the column-wall, and their length is fairly constant for the species. As a rule the longest thick-walled nematocysts occur in the stomodæum; those in the tentacles are as long or somewhat shorter; while they are the shortest in the disc, column-wall, and base. The longest nematocysts usually occur in the acrorhagi, or in any other special outgrowths of the column-wall which may be developed.

Usually it is only in the living polyps that the stinging-cells can be examined in their fully extruded state and their complete characteristics determined, including the swollen basal part and the simple or complex evaginated thread. But certain distinctions can be made out in macerations of preserved polyps, or even in sections. In the species now under investigation the occurrence and character of the stinging-cells are briefly as follows:—They are very sparingly represented in the basal ectoderm by an extremely small form of the thick-walled variety, measuring only .012 mm. In the column-wall they have been found only within the ectoderm of the evaginations. Here they are all of one kind: large, thick-walled, slightly curved, and varying in length from .038 mm. to .044 mm., with a diameter of about .008 mm.

The tentacular nematocysts include the two varieties. By far the majority are thin-walled with the spiral thread showing very distinctly, and are broad at one end and narrow at the other (fig. 8 *a*). They range in length from .018 mm. to .028 mm. The thick-walled form is numerous, and nearly as long as in the columnar evaginations, their

length varying from .034 mm. to .04 mm. They are invariably a little narrower than in the evaginations, measuring only .006 mm., and are nearly always perfectly straight.

In the disc stinging-cells are concentrated within the thickened lips, and are similar to the thin-walled representatives in the tentacles.

The nematocysts within the stomodæal ectoderm include only one representative of the curved columnar variety. They are very uniform in size, measuring .025 mm.

The mesenterial filaments are somewhat exceptional in being very sparingly supplied with nematocysts, even in the lower region. They are all narrow and straight, and are nearly of the same length as those in the stomodæum, namely .025 mm.

No nematoblasts occur anywhere within the endodermal epithelium.

It is thus clear that practically every region of the polyp possesses its own distinctive nematocyst. Though generally distributed throughout, the thick-walled variety differs slightly either in size or outline, or in both, in the different areas where it occurs. Examples intermediate in type are to be found mingled with the others, so that it is only when taken in numbers that the distinctive characteristics become of taxonomic value.

#### *Tentacles.*

As the column-wall is rarely overfolded in preserved polyps, and the tentacles are usually only slightly retracted, the latter are generally seen in their normal relationship in both vertical and transverse sections (Pl. 25. fig. 4 & Pl. 26. fig. 13). A transverse section, such as is represented in fig. 13, demonstrates that the tentacles are outgrowths of both the entocœlic and exocœlic mesenterial chambers. In some instances, as at  $t_4$  and  $t_5$ ,  $t_7$  and  $t_8$ ,  $t_{12}$  and  $t_{13}$ , it appears as if two tentacles originated side by side from a single mesenterial chamber, but on more close examination a pair of rudimentary mesenteries (III.) can always be detected, so that one of the tentacles is entocœlic and the other exocœlic. Such conditions prove that the appearance of a new mesenterial pair is followed very closely by the outgrowth of a tentacle from its entocœle. In the polyp from which fig. 13 was taken no exotentacles had as yet appeared between the entocœlic members  $t_5$  and  $t_6$ ,  $t_8$  and  $t_7$ ,  $t_{11}$  and  $t_{12}$ . For a short period, therefore, during the growth of new mesenteries, the number of tentacles may be less than the number of mesenteries, due to the lagging behind of the exotentacles; but in the end the sum is the same, a tentacle arising from each chamber, whether entocœlic or exocœlic.

The tentacular ectoderm and endoderm are both comparatively broad layers, but the mesogloea is very narrow. In sections the wall is about .055 mm. across. The ectoderm is usually thrown into minute rounded ridges separated by deep narrow grooves, the cells being elongated in the former and very short between (fig. 3). Nematocysts are distributed in a peripheral zone with approximate uniformity throughout the length of the tentacle, and are mainly of one kind: thin-walled, with the close spiral thread showing distinctly, and broad at one end and narrow at the other (fig. 8 a). Numerous examples of the larger, thick-walled variety, such as occurs in the evaginations, are also present, but are slightly shorter and much narrower.



The longitudinal ectodermal muscle is supported upon the mesogloea, which is usually thrown into slight folds to give it increased area, especially towards the proximal end. The nerve-ganglion layer is also clearly developed.

The endodermal epithelium is rather broad in the partly retracted tentacles, and exhibits an irregular free surface, while Zooxanthellæ are only sparsely distributed. The endodermal muscle (*end.m.*, fig. 3) is comparatively well developed, the mesogloea presenting delicate plaits for its support, best seen just above the tentacular septum (*t.c.s.*).

The tentacular cavity is separated from the general polypal cavity by a circular transverse partition, perforated in the middle, and situated a very short distance from the origin of the tentacles (figs. 3, 4, 6). The septum is covered on both sides by endoderm, and the supporting mesogloea is narrow and lined by delicate muscle-fibres on its inner and outer surfaces, continuous with the circular musculature of the tentacles. Its central free margin is thickened, and the mesogloea becomes plaited (*t.sph.*, figs. 3 & 6) in a sub-dendroid manner to afford additional support for the muscle-fibres, which here constitute a circular sphincter muscle. Various appearances of the partition in section, showing its relation to the cœlomic and tentacular cavities, are indicated in figs. 4 and 13, and the sphincter muscle (*t.sph.*), more highly magnified, in Pl. 25. figs. 3 and 6. Where in fig. 13 the section includes the middle of the partition the two free edges are seen to be in the main directed downwards into the polypal cavity, so that the membrane must be concave on its tentacular aspect and convex on its cœlomic side. In fig. 13, tentacles  $t_1$ ,  $t_2$ , and  $t_{10}$  are partly constricted at their origin, and such a condition has been noted among the external characters (fig. 1 c). No doubt the constriction is brought about by the action of the sphincter. In fig. 3 the tentacular wall immediately below the partition is seen to have become much thinned.

The presence of a tentaculo-cœlomic septum and sphincter has already been recognized in the genus *Bolocera*, including also the genus *Boloceroides* of Carlgren (1899, p. 43; 1900, p. 15). Carlgren (1893) describes and figures the formation at the base of the tentacles in *Bolocera longicornis*, and the musculature is there not much better developed than in *Bunodeopsis*. In *Bolocera* the contraction of the sphincter often leads to the detachment of the tentacles from the disc. In one or two of the Jamaica specimens of *Bunodeopsis globulifera* circular apertures occur in the tentacular zone, indicating that tentacles have disappeared therefrom, but I have never actually observed the process taking place in the living polyp. In *B. antillensis*, however, the tentacles were found to be readily detached on handling the polyps, and in this species also a tentacular septum and sphincter occur. Carlgren has pointed out that the partition comes off along with the tentacles, and such would certainly be presumed from the great narrowing which takes place immediately below the membrane, as represented in fig. 3.

McMurrich (1893, p. 154, pl. xxii. fig. 27) also describes and figures the tentacular sphincter in *Bolocera occidua*. In many of his specimens, mesenterial filaments were found protruding from the openings at the margin of the disc formed by the falling off of the tentacles. The same author includes the deciduous character of the tentacles

within the definition of the family Boloceridæ. Kwietniewski (1898, p. 394, pl. xxv. fig. 10) has also described and figured the sphincter in *Bolocera McMurrichi* (= *Boloceroides McMurrichi* (Kwietn.), Carlgren, 1899).

The occurrence of a perforated tentaculo-cœlomic septum and sphincter would appear to be somewhat restricted within the Actiniaria. So far, it is known only in the genera *Boloceroides*, *Bolocera*, and *Bunodeopsis*. Its presence would seem to be associated with deciduous tentacles, for the phenomenon is characteristic of all the forms above mentioned.

According to Carlgren (1899), the genera *Polystomidium* and *Polyopsis*, described by R. Hertwig in the report on the 'Challenger' Actiniaria as destitute of tentacles, are really *Bolocera* from which these organs have become detached. Haddon (1898) had independently come to the same conclusion. Carlgren suggests that the detachment of the tentacles may be a means of protection to the polyp.

McMurrich (1893) had already surmised, and later was able to confirm his suspicions by an actual examination of the specimens at the British Museum, that the 'Challenger' Actinian, *Liponema multififormum*, is also a *Bolocera*, from which the tentacles have been detached.

#### Disc.

The oral disc (*disc*, Pl. 25. figs. 4 & 6) is thin-walled peripherally, and continues thus until the lips are reached, when it becomes swollen before terminating at the stomodæum (*st.*). The discal ectoderm contains many clear gland-cells, and the radial muscle- and nerve-layers are comparatively well developed. At the lips the ectodermal cells are much longer, and thin-walled nematocysts occur, similar to those in the tentacular ectoderm, but stinging-cells appear to be absent from the remainder of the disc.

The discal mesogloa (fig. 6) is very narrow, and may be delicately plaited on both its outer and inner surfaces. At the lips it becomes much thickened and more strongly plaited, affording an increased area for the support of the circular endodermal muscle. This latter becomes so strongly developed as to constitute what must be regarded as a special endodermal circumoral sphincter (*or. sph.*, figs. 4 & 6). The action of the sphincter muscle must have become relaxed during the narcotization of the polyps, permitting the radial musculature to act, for in all the preserved specimens the oral aperture is large and rounded.

A sphincter muscle in this position is very exceptional among the Actiniæ, but a like concentration of muscle-fibres has been described by the brothers Dixon for *B. verrucosa* (1889, p. 322). It may be considered doubtful as to how far a special muscular development would be represented when the oral aperture returns to its living, slit-like condition.

Other than in its concentration of muscle-fibres the discal endoderm presents no special features. Comparatively few Zooxanthellæ are present.

#### Stomodæum.

The stomodæum is widely open in sections and usually somewhat irregular in outline (figs. 9-15). Its walls are very delicate, measuring only .045 mm. across. It is



comparatively long, extending into the gastro-cœlomic cavity for nearly one-half the height of the polyp, its inner free margin being reflected (Pl. 25. fig. 4). The ectoderm is often thrown into vertical folds, which are without any regular disposition, not necessarily corresponding with the mesenteries. The layer exhibits the same structure all the way round, being in no way modified to form special gonidial grooves opposite the directives. Prof. Verrill, in his description of the external characters of the Bermudas specimens, mentions the occurrence of gonidial grooves, but such are certainly not indicated in the histology of the stomodæum of the Jamaica representatives, and were not recognizable in the living polyps. In other species of Actiniæ where gonidial grooves occur, the ectoderm lining them usually offers a marked contrast with that along the lateral walls; the cilia are more strongly developed, and fewer gland-cells and nematocysts occur than elsewhere.

The stomodæal ectoderm (*ect.*, Pl. 25. fig. 7) is strongly and uniformly ciliated all round, and contains nematocysts (*nem.*) and granular gland-cells. The former are sparse towards the upper extremity, but as the lower free end is approached they become very numerous, and are all of the thick-walled variety, such as occur in the columnar evaginations, but slightly smaller, measuring .025 mm. in length. In the inner part of the layer they are irregularly arranged at all angles with the free edge, but towards the surface they become parallel with the other constituents. The ectodermal muscle (*ect.m.*) and ganglion-layer (*nr.l.*) are only feebly developed.

The mesogloea is extremely delicate throughout, and remains smooth on both sides. The endoderm closely resembles that lining the cœlomic cavity generally, and contains a few Zooxanthellæ in some places, while in others they are absent, in which latter case the epithelium is very narrow. The circular endodermal musculature is recognizable in vertical sections.

Intermesenterially the stomodæum narrows gradually towards its free lower extremity and becomes reflected, as on the left side of fig. 4; mesenterially the ectoderm appears continuous with the filament at the free edge of the perfect mesenteries. The stomodæal wall on the right side of fig. 4 terminates in a section of a mesenterial filament.

#### *Mesenteries.*

The mesenteries are very variable in number in the many polyps examined, and also in their cyclic relationships; for a long time it seemed impossible to establish any hexamerous or other regular system of arrangement. The conditions encountered will be best understood by reference to Pl. 26. figs. 9 to 15, representing outline sections through the stomodæal region of six different polyps.

In fig. 9 only three pairs of complete mesenteries occur, and two pairs which are incomplete. The lower complete pair (*d.*) are directive mesenteries, having the longitudinal muscle on the faces looking away from one another. The polyp from which fig. 10 was taken possessed three pairs of complete mesenteries, including a pair of directives and a single member of another complete pair. Within the wide interval on the right side are nine, short, incomplete mesenteries, which present some

indication of alternating large and small pairs. In this and the other figures the pairs are numbered according to the order to which they belong, so far as this can be determined with certainty. In the polyp whose mesenterial plan is represented by Pl. 26. fig. 11 a regularity of alternating complete and incomplete pairs is presented on the left side, but the right side is a region of irregularities. A mesentery also stretches across from one part of the column-wall to the other, and encloses a rudimentary mesenterial pair. In fig. 12 the left side possesses perfect dicyclic hexamerall symmetry, while the development at the upper right-hand region is very irregular. As before, many incomplete mesenteries occur at the upper right-hand corner.

Fig. 14 is the completed mesenterial plan of the polyp of which fig. 13 represents a little more than half. As before, the first and second cycles on the left side are regularly developed, and in addition three rudimentary pairs of the third cycle occur, a pair in each of the primary systems. The new pair in the dorso-lateral chamber is situated on the ventral aspect of the second cycle pair, but on the dorsal aspect in the middle and ventro-lateral chambers. On the right side the ventro-lateral system corresponds with that on the left, but the middle and dorsal systems are irregular.

Fig. 15 completes the series so far as I have been able to establish it. On the left side of the directive axis all the pairs of the first, second, and third orders of a hexamerall polyp are represented. The second-order mesenteries (II.), with the exception of the dorso-lateral pair, have reached the stomodæum. One mesentery only is missing on the right side from the number necessary to complete the hexamerall plan, but at the dorso-lateral region they are all incomplete and irregularly paired.

From the conditions thus presented there can be no doubt that normally the mesenteries should be arranged in alternating hexamerall cycles, with two pairs of directives, and that members of the second order should also reach the stomodæum. The increase in the number of the mesenteries, however, does not proceed throughout the polyp according to the usual order established for the Hexactinæ. According to this, the six primary pairs of mesenteries appear successively in a bilateral manner; then the members of the second cycle arise successively in unilateral pairs within the six primary exocæles, as a rule on each side of the polyp from the dorsal to the ventral aspect; the third cycle pairs appear as single unilateral pairs within one of the two exocæles in each of the six primary systems, and then later in the remaining exocæle in each primary system. In fig. 14 the sequence of the third cycle pairs seems to follow the rule that a pair is developed in each of the primary systems before a second pair arises to complete the radial symmetry.

All the figures of *Bunodeopsis* indicate that on one side of the polyp the increase takes place in a fairly normal and regular manner, but that such is not the case for the other side. In all the polyps a definite region of irregular growth occurs, both as to the number of mesenteries which are present and also as to their paired relationships. Evidently the hexamerall cyclic regularity becomes more pronounced as the polyps grow larger and the number of mesenteries increases, but I have met with no specimen in which perfect regularity was attained. Probably some of the polyps obtained are as

yet immature, but no larger were to be met with, and, judging from the number of tentacles and the dimensions, Verrill's Bermudas examples were in much the same condition as the Jamaican.

Undoubtedly the imperfect development of the tentacles within a restricted area, noticed among the external characters, is determined by the imperfect growth of the mesenteries. The two are associated phenomena; the rate of tentacular growth is regulated by that of the mesenteries, and where the latter are irregular the tentacles will be the same.

This regional irregularity of growth of the polyp would appear to be connected in some way with an asexual method of reproduction. In the more common *B. antilliensis* I have found that new polyps are produced by the process which Andres (1881) has described as "Scissiparity." Fragments of varying size become gradually detached from around the base of the column, attain an independent existence, and develop into new polyps with tentacles and oral disc. Andres has followed the process of development of the new individuals as it occurs in *Aiptasia lacerata*, and in this species the normal hexamerous disposition of the organs appears to be early assumed. I have not observed scissiparity in *B. globulifera*, but the other Jamaican species presents exactly the same tentacular and mesenterial irregularities.

Irregularities would be much more likely to occur in polyps thus originating than in individuals developed directly from the larva. The two species of *Bunodeopsis* occur in large numbers within restricted localities, and such a distribution is most probably the result of a like method of reproduction in each. The West Indian *Aiptasia tagetes* (Duch. & Mich.) also reproduces in a most prolific manner by scissiparity, and an examination of its mesenteries and tentacles reveals many departures from the hexamerous regularity. McMurrich (1889), on the other hand, describes the Bahamas representatives of this species as hexamerous, without mentioning any asexual reproduction. G. H. Parker (1899), who has made a detailed study of the effects of longitudinal fission in *Metridium marginatum*, finds the mesenteries are very irregularly arranged in what may be assumed to be fission polyps.

Returning to the individual mesenteries, the members of the first order are found to extend the whole length of the stomodæum, and some are continued as far as the base of the polyp, across which they extend to the middle (Pl. 25. fig. 4). The complete members of the second order may become free before reaching the stomodæal termination. At first the free edge of the mesenteries is straight, but soon it becomes greatly folded and contorted, some mesenteries becoming much more complex than others, so that they may appear several times in the same section (fig. 4). The incomplete mesenteries first appear in the uppermost part of the column-wall, but all except the youngest are better developed in the middle part of the polyp. Very often the mesenterial mesogloea and that of the column-wall are seen to be interrupted, the continuity of the circular endodermal muscle of the column-wall being thereby preserved (Pl. 26. fig. 17).

Within the stomodæal region of most polyps the mesenteries are extremely narrow, and, except at their origin in the column-wall, the musculature is so weak as to

be discerned with difficulty. Near its insertion in the column-wall the mesentery is usually a little broader, and the retractor muscle is represented as a smooth layer of fibrils. In other polyps the mesenteries are thicker, and muscle plaits are very distinct in the middle of their transverse length. Below the stomodæal region all the mesenteries become much broader, both the endoderm and mesogloea increasing in thickness, and the latter forms numerous plaitings for the support of the retractor muscles (*ret.m.*, Pl. 26. figs. 16 & 17). The retractor muscle in fact assumes somewhat of a circumscribed character, but the outline in transverse section is scarcely alike in any two mesenteries. For a short distance from the column-wall the muscle-band is smooth; the plaitings beyond are at first minute, then gradually become larger and more complicated, and terminate very abruptly, the mesentery afterwards being very narrow and continued for some distance (fig. 16). At the central termination of the complicated part of the muscle one or more of the mesogloæal plaitings may become greatly elongated and minutely plaited, almost as if the mesentery were about to branch (fig. 17, *ret.m.*).

The transverse musculature is comparatively strongly developed. In tangential sections near the base the mesogloea of the mesentery is irregularly folded for its support (fig. 2, *trans.m.*). When a complete mesentery is mounted as a microscopic object, the vertical and transverse muscle-fibrils are seen crossing one another at right angles.

The mesenterial endoderm is usually very narrow, and includes clear gland-cells and but few Zooxanthellæ. Traces of the nerve-layer, continuous with that on the column-wall, can usually be followed (*nr.l.*, fig. 16) for some distance beyond the insertion of the mesentery in the column-wall. In the lower region the mesenterial epithelium becomes swollen just behind the mesenterial filaments (*cf.* figs. 16 & 17), and in some polyps this region contains many clear spheroidal bodies, which stain very deeply and stand out as distinct objects from the rest of the tissue; a few small particles are black and irregularly shaped. Probably these foreign bodies are ingested nutrient particles, and they are practically absent from some individuals. Where present in quantity they may occur also in the endodermal epithelium of the lower part of the stomodæum, and sparsely in the endoderm of the column-wall, and even in the tentacular endodermal epithelium. The particles are easily distinguished by their homogeneous, deeply staining character from the Zooxanthellæ, which they greatly resemble in size and outline.

The swollen mesenterial endoderm immediately behind the mesenterial filament is generally regarded as a special region for intracellular digestion (McMurrich, 1899, p. 262), and in *Bunodeopsis* the greatest number of foreign particles occurs there; but their presence in other regions of the endoderm would imply that ingestion is by no means restricted to the region. The endodermal enlargements in the present species are often somewhat irregular in outline (fig. 17), not smoothly rounded as in most other forms.

At the origin of the mesenteries in the column-wall a delicate layer of muscle-fibrils, arranged nearly vertically, occurs on the face bearing the transverse musculature. This is the only trace of a parieto-basilar muscle; in no instance does the mesogloea become plaited or afford any indication of the formation of a pennon, such as is characteristic of Actinian species with a well-developed muscle.

A vertical section through a portion of the base, including a tangential section of a mesentery, is represented in Pl. 25. fig. 2. On the mesentery the mesogloal folds which support the transverse muscle (*trans.m.*) are strongly developed, and the muscle-fibres are seen in section. At the basal termination of the mesentery, however, no foldings are indicated; the muscle-layer is here perfectly smooth. Such an appearance can scarcely be regarded as in any way indicating an incipient basilar muscle, for no corresponding development takes place on the opposite face which bears the retractor muscle. In such sections, the muscle-fibres of the latter are seen lengthways. Where present in other species the basilar muscle is, as a rule, arranged on more or less strongly developed mesogloal plaitings on each side of the insertion of the mesentery on the base, the muscle-fibres extending in a radial direction. The present species is therefore characterized by possessing a parieto-basilar muscle of the weakest character, while the basilar muscle is altogether undeveloped.

The polyps are too small to permit of the presence or absence of mesenterial stomata being determined by means of dissection. But in serial transverse sections interruptions occur in all the perfect mesenteries close to the stomodæum and at its upper extremity. These represent the inner or perioral stomata, but no corresponding series has been found near the column-wall, such as may represent the outer parietal stomata.

#### *Mesenterial Filaments.*

Mesenterial filaments occur at the free edge of all the mesenteries except the most rudimentary. They appear on the complete mesenteries as these sever their connection with the stomodæum, while usually they are not developed on the incomplete mesenteries until below the stomodæal region. The filaments follow the contortions of the free edge of the mesenteries, so that in the lower part of the polypal cavity the filament belonging to one of the mesenteries may be seen cut through several times in the same section (fig. 4).

The filaments on the complete mesenteries are at first trilobed and exceptionally wide, and both the glandular streak and ciliated bands are clearly represented (fig. 18). The ciliated bands are far apart, and the tissue intermediate between them and the glandular streak is irregularly thickened, so that the outline assumed by the filaments is somewhat exceptional among the Actiniæ, and varies greatly in different sections. A little within the base of the filament the mesenterial mesogloa divides into three very narrow branches, each of which passes into a lobe, and there terminates in a clear expansion, practically devoid of any cell-enclosures.

The middle portion of the trefoil is low, and the glandular streak at its apex (*g.s.*, fig. 18) is at first quite rudimentary in the degree of its development, merely capping the middle of the filament as a more densely staining tissue. In addition to the supporting cells, the glandular streak contains a few granular gland-cells and thick-walled nematocysts.

On each side of the glandular streak, and sharply separated from it, occurs an accumulation of undifferentiated endodermal-like cells, rarely regular in its outline, recalling in



this respect the irregular endodermal thickenings on the mesenteries immediately behind the simple filaments. The cells are much vacuolated, and here and there Zooxanthellæ may occur. To this tissue (*i.s.*, fig. 18), which is partly developed on both the middle and lateral lobes of the filament, and separates the glandular streak from the ciliated bands, I have already (1900, p. 146) given the name of *intermediate streak*. It is recognizable in most trilobed Actinian filaments, and McMurrich (1899, p. 259), in describing the filaments of *Zoanthus sociatus*, has also independently applied the designation *intermediate epithelium* to what appears to be the corresponding tissue in the Zoanthean filament. In the present species it often appears as if folding over or partly covering the first portion of the ciliated bands, and is more truly endodermal in character than in most Actiniæ. In some longitudinal sections through the filaments it presents a distinctly banded appearance, with the deeply staining tissue of the ciliated bands at the bottom of the depressions, as is so well displayed in McMurrich's figures of *Z. sociatus* (1899, p. 259).

The ciliated bands are strongly developed and nearly encircle the lateral mesogloæal lobes. They are constituted altogether of ciliated supporting cells. On the front face of the lateral mesogloæal axes they are continued in many transverse sections as a very narrow band towards the middle of the filament, diminishing all the way, and overlaid by the intermediate epithelium, as represented in fig. 18. In other sections the prolongations are not recognizable. Posteriorly the ciliated bands pass into what I have termed the *reticular streak*, which here closely resembles the mesenterial epithelium and is continuous with it.

In the glandular, intermediate, and ciliated areas the trilobed mesenterial filament thus presents three wholly distinct varieties of cellular tissue. That constituting the glandular streak bears the closest resemblance to the stomodæal ectoderm; the intermediate tissue is in no way distinguishable from the endodermal epithelium; while that of the ciliated bands, consisting wholly of long narrow supporting cells, is very specialized and different from any other of the polypal tissues.

Prof. McMurrich in his study of the mesenterial filament of *Z. sociatus* has devoted special attention to the relationship of the ciliated bands and the intermediate region. With its long, well-developed filaments, the species is specially fitted for such an investigation. Discussing the endodermal origin or otherwise of the intermediate epithelium, McMurrich affirms that it is certainly continuous with the stomodæal ectoderm above, and not with the endoderm, and from all the evidence before him is inclined to regard it as being ectodermal like the rest of the ciliated band epithelium. So far as histological evidence can be depended upon, an endodermal origin would be assigned it in the present species; in character it is wholly distinct from the ciliated and glandular streaks and stomodæal ectoderm.

The trilobed condition of the mesenterial filaments in *Bunodeopsis* is continued only for a short distance down the mesenteries, when it becomes replaced by the simple filament; but the species is not suitable for tracing the actual passage from the one to the other. McMurrich (p. 264) states "that in *Z. sociatus* there is neither a histological continuity

nor a histological identity of the upper part of the median streak of the filament with the lower or glandular streak proper." Embryological considerations also point to the conclusion that a different origin must be assigned the apical median part of the mesenterial filament in the uppermost region as compared with the whole filament below. From the researches of McMurrich, H. V. Wilson (1888), Appellöf (1900), and myself (1899), there is good reason to suppose that the former is a downgrowth of the stomodæal ectoderm, according to my interpretation, to meet the upgrowing endodermal filament.

In *Bunodeopsis* the ciliated bands quickly disappear along with the two lateral mesogloal lobes which supported them, and the simple filament remaining is altogether different from the middle lobe of the more complex filament, although it corresponds with it in position, representing as it does the termination of the free edge of the mesentery. The unmodified endodermal tissue, which constituted the intermediate streak of the complex filament, and covered the middle lobe laterally, is likewise no longer represented in the simple lobe (Pl. 26. fig. 16).

The cellular constituents along the front and sides of the simple filament, however, most closely recall those of the glandular streak of the compound filament, consisting mainly of ciliated supporting cells and coarsely granular gland-cells, with the addition of a few thick-walled nematocysts. The posterior part of the filament on both sides is constituted of much shorter cells, which seem to be all ciliated supporting cells, no nematocysts nor gland-cells being recognizable. Histologically, and probably physiologically, the hinder region of the simple filament most nearly approaches the ciliated bands, though no morphological identity seems possible.

At first the mesenterial mesogloea as it enters the posterior part of the filament remains swollen as in the trilobed filament, but in the lower part of the filament it becomes flattened and rapidly thins out at each side. The anterior surface of the mesogloea is provided with a layer of extremely delicate muscular fibrils.

In the lower region of the polyp the filaments and free edge of the mesenteries are greatly folded and contorted, but they by no means crowd the gastro-coelomic cavity (Pl. 25. fig. 4).

No gonads were developed within any of the polyps examined.

In its essential features, *B. globulifera* closely resembles *B. strumosa* and *B. antilliensis*, which were incompletely described in the paper (1897) "The Actinarian Family Aliciidae." An important external specific distinction is that the columnar evaginations in the first are smooth and thick-walled throughout, while in the two older species they are thin-walled in places, and the large nematocysts occur in restricted thickened bands or tubercles. In sections this difference is indicated by the practical uniformity in thickness of the ectodermal evaginations of *globulifera* (fig. 5), and their alternating narrow and broad outline in *strumosa* and *antilliensis*, according as nematocysts are absent or present.



The three agree in such important characteristics as the presence of an ectodermal columnar and stomodæal muscle- and ganglion-layer, the absence of gonidial grooves, the absence of a basilar muscle and of a well-developed parieto-basilar and endodermal sphincter muscle, and the presence of ciliated bands on the mesenterial filaments.

In accordance with these later results, the definition of the genus *Bunodeopsis* may be emended as follows :—

Genus *BUNODEOPSIS*, Andres.

Actiniaria with ciliated flattened base, feebly adherent. Column-wall beset proximally with simple or complex, sessile or pedunculated evaginations, bearing large thick-walled nematocysts; distal part of column smooth and delicate. Column with ectodermal and endodermal muscle- and ganglion-layers; sphincter muscle very feeble or absent. Tentacles elongated, deciduous, separated from the polypal cavity by a circular perforated septum provided with a sphincter muscle. Disc with thickened lips and circumoral sphincter muscle. Stomodæum with ectodermal muscle and ganglion-layers, without gonidial grooves.

Mesenteries normally hexamerous, two pairs of directives, more than six complete pairs, often irregularly developed. Parieto-basilar muscle very feeble. Basilar muscle absent. Mesenterial filaments with ciliated bands. Without acontia and cinclides.

From the foregoing account it is clear that, while in many respects *B. globulifera* possesses primitive Actinian characteristics, yet in others it is highly differentiated. If the conclusions of Carlgren (1900) as to the nature of the primitive Actiniæ be correct, among the former must be reckoned the occurrence of an ectodermal columnar and stomodæal muscle- and nerve-layer, the absence of gonidial grooves from the stomodæum, the absence of a basilar muscle, and the weakness of the internal musculature generally. Among the latter will be included the division of the column into two distinct regions, of which the upper is naked, and the lower bears hollow evaginations with the ectoderm broadened and charged with thick-walled nematocysts; the occurrence of a tentaculo-cœlomic septum provided with a sphincter muscle; the circumoral ectodermal thickening (lips) charged with thin-walled nematocysts; the circumoral endodermal sphincter muscle; and the regional differentiation of growth of the tentacles and mesenteries.

The first-mentioned characters are those upon which Carlgren has founded the Tribe Protanthæ, which includes the lowest Actiniæ, as contrasted with the Tribe Nynanthæ, under which are placed all the more differentiated Actiniæ. Carlgren regards as the most important characteristic of the Protanthæ the presence of the ectodermal longitudinal muscle- and nerve-layer in the column-wall, and gives second place to the absence of the basilar muscle. Wherever the first-mentioned structures occur, Carlgren would separate their possessors from the forms with which they have been associated, and place them under the Protanthæ, whatever the other characteristics of the species might be.

In a forthcoming report on the Porto Rican Actinians, to be published by the U.S. Fish Commission, I have discussed these proposals somewhat, so that it is

unnecessary to here enter into the subject in detail, except as concerns its bearing on the present species. Suffice it to say that, while disposed to recognize the primary character of the ectodermal columnar musculature in Actiniæ, writers such as McMurrich, Haddon, and van Beneden are not prepared to accord it the taxonomic importance which Carlgren claims for it. Rather they would regard any species in which such a structure is retained as among the lowest members of its own particular group. And this is the view which seems most likely to result in a natural grouping of the Actiniaria, one which will recognize both the primitive and the differentiated characteristics of a species.

Undoubtedly characteristics such as the presence of the ectodermal columnar musculature, the absence of a basilar muscle, and of ciliated bands from the mesenterial filaments, are in themselves of vastly greater phylogenetic value than such features as columnar modifications, the origin of one or more tentacles from a mesenterial chamber, the nature of the sphincter muscle, the number and characteristics of the mesenteries, &c. But these latter are the differentiations which alone are available for classificatory purposes within the Nynanthæ, and to wholly separate the lowest forms possessing them would seem to take away the possibility of a phylogenetic grouping. The possessors of the ectodermal columnar musculature do not appear to represent a homogeneous assemblage.

*Bunodeopsis* is a good example of a genus in which, while certain primitive characteristics are retained, important structural modifications have taken place in other respects. To arrange it with others, on account of the former alone, would be to neglect those differentiations upon which the classification of the Actiniæ is mainly founded.

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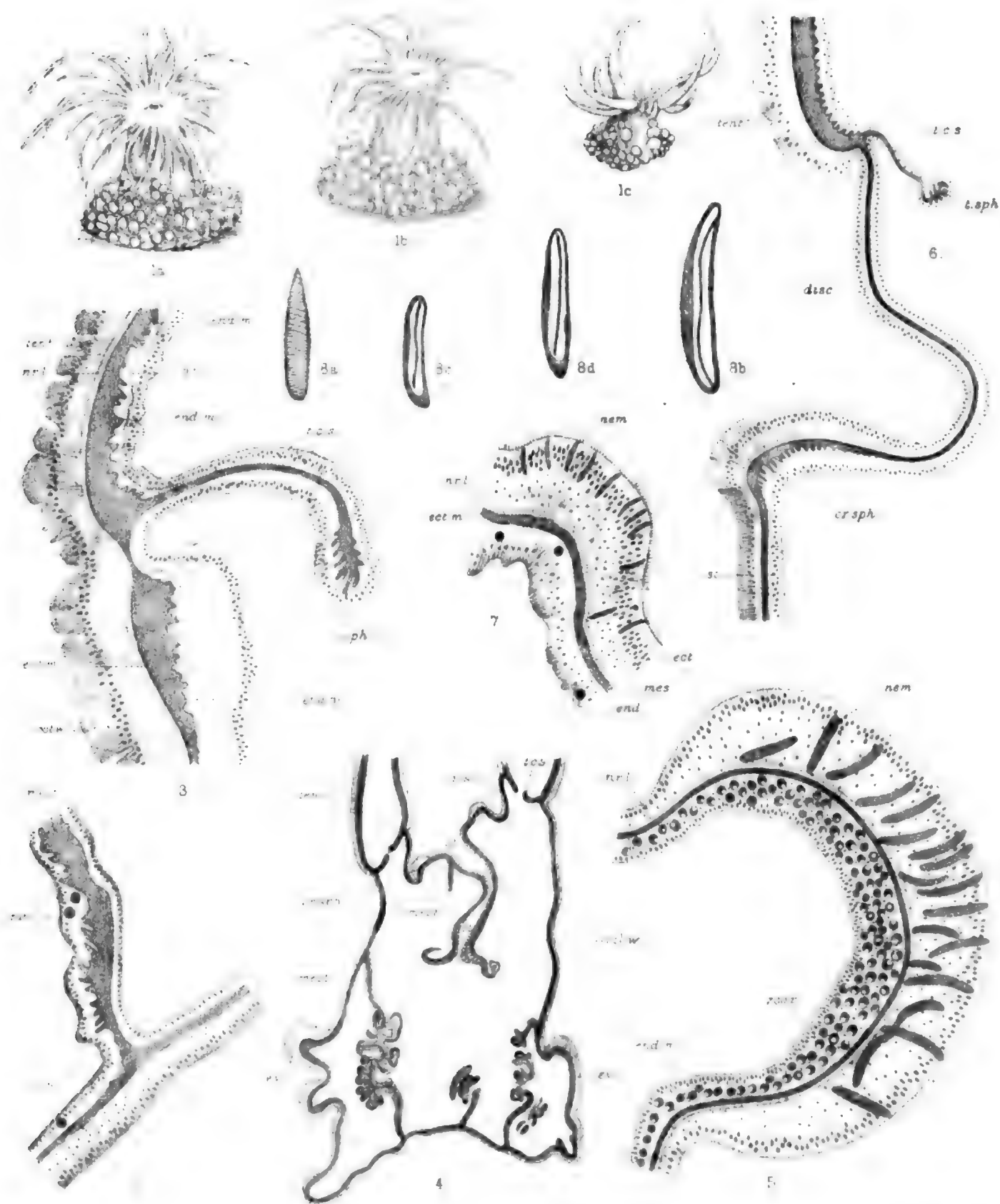
## EXPLANATION OF PLATES 25 & 26.

### Reference letters.

I., II., III., = orders of mesenteries. *c.s.* = ciliated band. *col.w.* = column-wall. *d.* = directive mesenteries. *disc* = disc. *ect.* = ectoderm. *ect.m.* = ectodermal muscle. *end.* = endoderm. *end.m.* = endodermal muscle. *ev.* = columnar evagination. *g.s.* = glandular streak. *i.s.* = intermediate streak. *mes.* = mesogloea. *mesl.* = mesentery. *m.fil.* = mesenterial filament. *nem.* = nematocyst. *nr.l.* = nerve-layer. *or.sph.* = oral sphincter. *ret.m.* = retractor muscle. *st.* = stomodæum. *t.c.s.* = tentaculo-cœlomic septum. *t.*, *tenl.* = tentacle. *t.sph.* = tentacular sphincter. *trans.m.* = transverse muscle. *zoox.* = Zooxanthellæ.

- Fig. 1, *a, b, c*. Three different polyps, somewhat enlarged: *a* and *b* in the living expanded condition; *c*, a preserved polyp.
2. Vertical section through a portion of the basal disc, including a tangential section of a mesentery. No basilar muscle occurs at the insertion of the mesentery on the basal wall.  $\times 400$ .
  3. Vertical section through the upper region of a polyp, including a part of one side of a tentacle, the upper part of the column-wall, and one side of the tentaculo-cœlomic partition with the tentacular sphincter at its free extremity. The polypal wall in all its three layers is here more swollen than usual.  $\times 400$ .
  4. Median vertical section through an entire polyp, but including only the basal part of two tentacles. The stomodæum is slightly protruding, and several mesenteries are cut obliquely.  $\times 70$ .
  5. Vertical section through a columnar evagination.  $\times 400$ .

- Fig. 6. Vertical section through the basal part of a tentacle with the tentaculo-cœlomic septum attached, the disc, and upper portion of the stomodæal wall.  $\times 300$ .
7. Transverse section through a portion of the stomodæal wall.  $\times 400$ .
8. Nematocysts: *a*, thin-walled form from the tentacular ectoderm; *b*, thick-walled form from the columnar evaginations; *c*, from the stomodæum; *d*, from the mesenterial filaments.  $\times 1200$ .
9. Transverse section of a polyp with only three pairs of complete mesenteries.  $\times 70$ .
10. Transverse section of a polyp with three pairs of complete mesenteries, one moiety of another pair, and at one region numerous incomplete pairs.  $\times 70$ .
11. Transverse section of a polyp with four pairs of complete mesenteries, a moiety of two other pairs, and a region with many incomplete pairs. A section of a tentacle which has intruded within the polypal cavity is represented at the upper right-hand corner.  $\times 70$ .
12. Transverse section of a polyp in which for the most part hexameral regularity prevails, but at one region growth is proceeding irregularly.  $\times 70$ .
13. Transverse section through part of the stomodæal region of a polyp, including the tentacular zone. The relations of the tentacles to the mesenterial chambers and the tentaculo-cœlomic septa are clearly shown.  $\times 70$ .
14. Transverse section of the same polyp at a slightly lower level. Mesenterial pairs belonging to the first, second, and third orders occur regularly throughout the greater part of the polyp, but the sequence is irregular at the upper right-hand side.  $\times 70$ .
15. Transverse section of a large polyp in which three orders of mesenteries are regularly developed, except on the right upper side. Most of the pairs of the second order have become inserted on the stomodæum.  $\times 70$ .
16. Transverse section of a portion of the column-wall a little below the stomodæal region, with a mesentery attached, bearing a simple mesenterial filament.  $\times 400$ .
17. Transverse section of a mesentery and the portion of the column-wall to which it is attached.  $\times 300$ .
18. Transverse section through a trilobed mesenterial filament.  $\times 400$ .



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X. *On the Morphology of the Brain in the Mammalia, with Special Reference to that of the Lemurs, Recent and Extinct.* By G. ELLIOT SMITH, M.D. (Sydney), Fellow of St. John's College, Cambridge, and Professor of Anatomy, Egyptian Government School of Medicine, Cairo. (Communicated by Prof. G. B. HOWES, D.Sc., LL.D., F.R.S., Sec. Linn. Soc.)

(With 66 Illustrations in the Text.)

Read 6th March, 1902.

#### INTRODUCTION.

THIS investigation was undertaken primarily to consider the possibility of homologizing the sulci of the cerebral hemisphere in different Orders of Mammals. With this object in view, the brain was examined in almost every genus in the whole class of Mammalia; but as this yielded such an immense and unwieldy mass of data, it became necessary, both for the sake of clearness and conciseness of exposition as well as to admit of the adequate discussion of the significance of the facts, to limit the scope of the enquiry, or, rather, to select the most instructive body of evidence which might typify the conclusions to be drawn from a study of the whole mass of data.

This process of curtailment has been accomplished in two ways. In the first place, attention has been almost wholly concentrated on the consideration of the homologies of the furrows called "calcarine" and "Sylvian." These are the only sulci (in addition, of course, to the hippocampal and rhinal fissures) which are absolutely constant in all Primates. At the outset of this investigation it became abundantly evident, firstly, that if the calcarine sulcus is a distinctive feature of the Primates and is not represented in the brain of other Mammalia, the search for homologues of the other, less stable, furrow on the mesial surface of the hemisphere must *à fortiori* be utterly futile; and, secondly, if the Sylvian fissure of the Apes and Man is represented in other mammals by no sulcus other than that inconstant and exceedingly unstable series of *different*\* furrows, which in various Carnivores, Ungulates, Edentates, Rodents, and Marsupials is commonly called "Sylvian," the possibility of homologizing any sulcus on the lateral aspect of the hemisphere of the Primates with a furrow on the surface of the brain of other mammals becomes utterly destroyed. That this not altogether obvious conclusion must inevitably be drawn from the premiss just stated will be abundantly shown in the following pages. We shall, therefore, best arrive at some decision regarding the main question, by devoting our attention chiefly to the Sylvian and calcarine furrows, without, however, altogether neglecting the other sulci. In the second place, I have deemed it desirable to further limit the dimensions of this work, by restricting the detailed account

\* Non-homologous.



of the sulci (and the organ in which they occur) to one circumscribed group of mammals; and, so as not to also narrow the scope of this discussion by so doing, I have freely introduced comparative data, which serve to indicate the behaviour of each individual sulcus in the whole Mammalian class.

The brain of the Lemurs has been selected as the aptest expression of these requirements. I can best explain this by anticipating some of the conclusions of this research. The features of the Prosimian brain become really intelligible only on the supposition that the Lemurs have advanced a considerable distance in the main stream of the evolution of the Primates and have then retrograded; among other manifestations of this retrogressive process many interesting phases of the disintegration of the cerebral sulci are exhibited, so that it becomes possible to recognize the constituent elements of many compound sulci in the Primates, and so the more readily to compare them with the furrows found in other mammals.

My choice of the Lemurs was further confirmed by other considerations of a very different nature. The opportunity of examining a much more representative collection of Prosimian brains than had previously fallen to the lot of any one observer, and the unique facilities for studying the brain-form of the extinct Lemuroids, for which I am indebted to the kindness of Dr. Forsyth Major, were additional reasons for choosing the brain of the Lemurs as the touchstone on which to test the hypotheses suggested by a study of the brain of other mammals. Moreover, the present state of our knowledge of the mammalian brain is so unsatisfactory, that no apology would be necessary for discussing its apparently obvious features in any Order, and least of all in the enigmatical family of Lemurs; for in no group of mammals is accurate knowledge of the brain more urgently wanted than in the latter. The voluminous literature of the Prosimian brain is particularly barren so far as exact and authentic statements of fact are concerned, and unduly rich in the grossest inaccuracies.

The foregoing statement of the object of these notes will explain their nature and scope. They do not pretend to be a monograph on the Prosimian brain, but are rather an account of the more variable features of the mammalian brain, as these are exhibited in the Lemurs. I have deemed it advisable, if for no other purpose than to give some idea of the "setting" of the pattern of the cerebral convolutions, to give a brief account of the outstanding features of the brain as a whole. The morphology of the mammalian cerebellum is incidentally discussed also.

In attempting to settle such an essentially morphological problem as the search after a fundamental plan underlying the apparently heterogeneous maze of cerebral sulci found in the different Orders, the observer is afforded an excellent opportunity of appreciating at their true worth the factors which disguise the common plan. The value of the evidence of the brain as an indication of the closeness of the bonds of affinity between the Lemurs and other mammals hence falls not unnaturally within the scope of this study.

## THE LITERATURE \*.

Since Tiedemann † first described the brain of *Lemur mongoz*, a very considerable number of memoirs on the Prosimian brain have been published. The interest of the numerous early descriptions, which include those of Leuret (1839), Schroeder van der Kolk and Vrolik (1846-54), and van der Hoeven and van Camper (1859), is almost purely historical. But the same period yielded an excellent memoir by Burmeister on the brain of *Tarsius* ‡, which represents to the present day all the accurate information we possess concerning this brain. It is of further interest as the first really valuable contribution to our knowledge of the Prosimian brain.

The most critically-careful descriptions of any Lemurs' brains are contained in the two memoirs of W. H. Flower §, which include brief accounts of the brain in *Lemur fulvus* [*nigrifrons*] and *Nycticebus tardigradus*, with notes on that of a *Galago*.

In 1886 Richard Owen published the first account of the brain of *Chiromys*, in a memoir || which lacks the clearness and definiteness of Flower's monographs.

In 1872 Paul Gervais gave an interesting account of the shape of the brain in the various genera of Lemurs from the data supplied by the study of cranial casts ¶; but as he made little or no attempt \*\* to check the results of his examination of the cranial moulds by comparison with the actual brains, he draws many inferences concerning the latter, and also with regard to the affinities of the Lemurs (see the title of his memoir !), which are not justified by a study of the brain itself.

In 1875 A. Milne-Edwards gave an account of the brain in the Indrisinæ ††, which represents all the published data concerning the actual brains in the genera *Indris*, *Propithecus*, and *Avahis*. [Many recent writers (such as Flatau and Jacobsohn, whose acquaintance with the bibliography of their subject is as slight as their knowledge of the actual mammalian brain) attribute the knowledge of the brain in *Indris* to Chudzinski, who borrowed from Milne-Edwards's monograph, and to Zuckerkandl, who makes the merest reference to the brain of *Propithecus diadema* ‡‡.]

\* Several of the titles, more especially of the earlier memoirs, are not given in this list. When recently in England I read the whole literature of the Prosimian brain, excepting only the memoir of Bischoff, which I unintentionally overlooked. But I neglected to make any notes on such memoirs as contained no information of any value, and even neglected the titles of some. To an exile from the lands of libraries, the gifts of reprints such as I have to acknowledge from Dr. Forsyth Major, Mr. Boddard, and Professor Burckhardt are especially welcome.

† 'Icones Cerebri Simiarum et quorundam Mammalium rariorum,' Heidelberg, 1821.

‡ 'Beiträge zur näheren Kenntniss der Gattung *Tarsius*,' Berlin, 1846.

§ "On the Posterior Lobes of the Cerebrum of the *Quadrumanus*," Phil. Trans. 1862; and "On the Brain of the Javan Loris (*Stenops javanicus*, Illig.)," Trans. Zool. Soc. 1866.

|| "On the Aye-aye," Trans. Zool. Soc., vol. v. 1866, pp. 68 et seq.

¶ "Mémoires sur les formes cérébrales propres à l'ordre des Lémures," Journal de Zoologie, tome i.

\*\* He refers to an earlier account of a Lemur's brain in his Hist. d. Mammifères, which I have had no opportunity of consulting.

†† In Grandidier's 'Histoire Physique, Naturelle et Politique de Madagascar,' (2) tome vi. texte (Paris, 1875).

‡‡ E. Zuckerkandl, 'Ueber das Reicheentrum,' Stuttgart, 1887, Taf. 3. fig. 28 (pp. 29, 45, & 70).

More recent numbers of the 'Histoire' contain illustrations of the brain in the genera *Lemur*, *Hapalemur*, and *Lepidolemur*.

The references to this will be found below in the accounts of these genera.

I have not seen Wernicke's short account \* of the brain of *Lemur fulvus* [mongoz], and know of it merely from the passing references in three of the more recent memoirs quoted below.

In 1890 J. T. Oudemans gave us the best account we possess of the brain of the Aye-aye †; and in the same year W. Turner examined ‡ in the light of comparative data Flower's above-quoted accounts of the Lemur's brain.

F. E. Beddard published an account of the brain of *Hapalemur griseus* in 1891, of those of an extensive series of various species of *Lemur*, *Galago*, *Chirogale*, *Loris*, *Nycticebus*, and *Perodicticus* in 1895, and those of *Hapalemur simus* and another *Hapalemur griseus* this year (1901) §.

In 1895 the first of Théophile Chudzinski's extraordinary memoirs || made its appearance. It is a most peculiar document. The writer discusses the brains of *Lemur*, *Indris*, and what he calls *Loris gracilis*. The data for the first two are apparently borrowed from Flower's and Milne-Edwards's memoirs ¶; and the third—the only one which the author himself describes—certainly belongs not to *Loris gracilis*, but to *Nycticebus tardigradus*. This error is the more singular because the author prefaces his description with the remark that "it is easy, with a little practice, to recognize without any difficulty the Order, Family, Genus, and often even the Species, to which a particular brain belongs" (p. 435). His second memoir, which deals with the brain of *Chiromys*, is so vaguely written and so poorly illustrated as to be almost valueless.

In the same year (1896) Theodor Ziehen gave an account of the cerebral hemispheres of a large number of Lemurs, the nucleus of which consists of the collection in the Royal College of Surgeons \*\*.

In 1889 Flatau and Jacobsohn gave a detailed account †† of the whole brain of a *Lemur macaco* [or "*macao*," as they spell it throughout their book], and of a second brain

\* Archiv für Psychiatrie, Bd. vi. Taf. 4. fig. 10.

† "Beiträge zur Kenntniss des *Chiromys malagascariensis*, Cuv.," Natuurk. Verh. der Koninkl. Akademie. Amsterdam, Deel xxvii.

‡ "The Convolutions of the Brain," Journal of Anatomy and Physiology, vol. xxv.

§ "Additional Notes upon *Hapalemur griseus*," Proc. Zool. Soc. 1891, p. 456. "On the Brain in the Lemurs," Proc. Zool. Soc. 1895, pp. 142 *et seq.* "Notes on the Broad-nosed Lemur, *Hapalemur simus*," Proc. Zool. Soc. 1901, p. 127. Compare also "On certain Points in the Anatomy of *Callithrix torquata*," Novitates Zoologicae, vol. viii. Oct. 1901.

|| "Sur les plis cérébraux des Lémuriens en général et du *Loris grise* en particulier," Bull. de la Soc. d'Anthropol. de Paris, 4<sup>e</sup> série, tome vi. 1895, pp. 434–464. "Sur les plis cérébraux d'un Aye-aye (*Chiromys, Mysipitheus*, Siegenat)," *ibid.* tome vii. 1896, pp. 12 *et seq.*

¶ I make this statement from memory, as I am now unable to consult the original.

\*\* "Ueber die Grosshirnfurchung der Halbaffen und die Deutung einiger Furchen des menschlichen Gehirns," Arch. f. Psychiatrie, Bd. xxviii. 1896, pp. 898 *et seq.*

†† "Handbuch der Anatomie und vergleichenden Anatomie des Centralnervensystems der Säugethiere," 1 Teil. Berlin, 1889.

which they call "*Stenops gracilis*." There can, however, be little doubt that the ambitious authors of this extraordinarily inaccurate book have followed in the footsteps of Chudzinski, and have mistaken *Stenops* [*Nycticebus*] for *Loris*.

In the instructive memoir on the insula in the Carnivora which M. Holl \* published in 1899, there is an interesting figure representing the lateral aspect of the right cerebral hemisphere of a Lemur of unknown species.

In 1900 E. Zuckerkandl † gave a brief account of the structure which he calls by the misleading title "Balkenwindung" in four species of the genus *Lemur* and in *Chiromys*; and in the same year the most extraordinary contribution to the literature relating to the Prosimian brain was published ‡.

In addition to Turner, to whose memoir reference has already been made, several other writers have discussed the anatomy of the Lemur's brain, without apparently adding any new data to the common stock.

The writings of A. J. Parker § and Gegenbaur || belong to this category.

Dr. Forsyth Major has described the form of the brain in two sub-fossil Lemuroids ¶; and Rudolph Burckhardt has published some most extraordinary criticisms of Forsyth Major's memoir, in the course of which he commits the blunders which he erroneously accuses the latter of perpetrating.

Max Weber, and in a lesser degree Eugène Dubois and Theodor Ziehen, have investigated the weight of the brain in the various Prosimian genera. Their results are discussed in the body of this Memoir.

The nucleus of the material upon which this account is based consists of four brains of *Lemur fulvus* [labelled *mongoz*, *albifrons*, and two of them *nigrifrons*], and one each of *Lemur varius*, *Lemur catta*, *Nycticebus tardigradus*, *Loris gracilis*, *Perodicticus potto*, *Galago Garnetti*, *Galago crassicaudata*, and *Microcebus Smithi*, in the Collection of the Royal College of Surgeons in London. These are the same brains upon which Ziehen's memoir was based; but as I found it necessary to remove the pia and arachnoid membranes before I could properly see the surface of any of these specimens, the reader will appreciate one of the reasons for any discrepancies which may be found in the two accounts of the same specimens.

Since Ziehen's visit to the College of Surgeons two brains of *Chiromys* have been placed in the Galleries. One of these was found in the College Stores and the other was purchased from the Zoological Society, Mr. Beddard kindly consenting to part with his

\* "Ueber die Insel des Carnivorengehirns," Arch. f. Anat. u. Phys., Anat. Abth., Taf. 12. fig. 16.

† "Beiträge zur Anatomie des Reicheentrums," Sitzungsberichte d. kaiserl. Akad. der Wissensch. in Wien, Math.-naturw. Cl., Bd. cix. Abth. iii., July 1900, p. 2.

‡ Henry C. Chapman, "Observations upon the Anatomy of *Hylolates leuciscus* and *Chiromys madagascariensis*," Proc. Acad. Nat. Sci. Philadelphia, May 1900, p. 420.

§ "Morphology of the Cerebral Convolution, with Special Reference to the Order of Primates," Journ. Acad. Nat. Sci. Philadelphia, 2nd series, vol. x. (1896).

|| "Vergleich. Anat. der Wirbelthiere," i. Bd., Leipzig, 1893, pp. 766 & 767.

¶ "On the Brains of two Sub-Fossil Malagasy Lemuroids," Proc. Roy. Soc. vol. 62 (1897), pp. 46-50.

specimen, so that one anatomist might have the chance of describing and comparing the two brains. Dr. Charles Hose has from time to time sent to Mr. W. L. H. Duckworth in Cambridge a valuable series of excellently preserved brains from Borneo, which I have had an opportunity of examining. Mr. Duckworth very generously placed at my disposal two brains of *Tarsius*, one of which had been fixed and preserved *in situ* by means of formalin injections, and the other had been extracted with all that care and skill for which Mr. Hose is so well known among zoologists. This brain was preserved for histological purposes in Müller's fluid. Mr. Duckworth also permitted me to examine many other specimens, including an excellent brain of *Galago Garnetti*. Captain Stanley Flower has kindly placed at my disposal the fresh bodies of five Lemurs and a *Nycticebus* which died in the Ghizeh Zoological Gardens during the last few months, and I have thus been able to examine the brain of these animals in a perfectly fresh condition. He has also given me skulls of *Lemur macaco* and *Nycticebus tardigradus*. From these I have been able to make cranial casts.

Dr. Forsyth Major, whose generous help has been afforded me in many ways during the course of this investigation, gave me the brain of *Microcebus Smithi* and lent me the skulls of various Lemurs. On his suggestion, the authorities in the Geological and Zoological Departments of the British Museum kindly permitted me to examine their large collections of crania of recent and extinct Lemurs. I have also examined all the crania of Prosimiæ in the collection at the Royal College of Surgeons.

I have thus been able to study the shape of the brain and the arrangement of the cerebral furrows not only in every genus and most species of recent Lemurs, but also in the extinct *Lemur Julliyi*, *Globilemur*, and both an adult and a young *Megaladapis*. As Dr. Forsyth Major was engaged in investigating these valuable extinct forms, my indebtedness to him is all the greater for allowing me to examine them.

It is commonly supposed that a mould of the cranial cavity can give little exact information beyond indicating the shape of the brain. In most Apes this is to a very great extent true. But in most mammals in which the pattern formed by the sulci is not very complex (and also even in some, especially Carnivores, in which a very rich supply of sulci exists) a series of prominent ridges develop on the inner face of the cranial wall so as to accurately map out the plan of the sulci. These ridges are especially well developed in all Lemurs, excepting only the extinct form *Globilemur*, in which the pattern becomes blurred as in most Apes.

It is, however, absolutely necessary, if one is to accurately interpret the plan of the sulci from the arrangement of these bony ridges, to carefully study the actual brains of several genera and the crania in which they were lodged, to appreciate several sources of fallacy, which have been so unfortunately demonstrated in Gervais's uncontrolled study of casts (*op. cit. supra*). If this precaution be taken, one is able to map out the plan of the sulci on the outer surface of the hemisphere in a plaster mould with the certain conviction that he is accurately interpreting the configuration of the brain itself.

From the specimens (*Lemur*, *Nycticebus*, *Microcebus*, and *Tarsius*) which I have been able to devote to histological purposes, I have been able to determine many interesting features in the arrangement of the fibre-tracts, especially the optic and olfactory paths

in the cerebral hemispheres and the anatomy of the pyramidal tracts. But as these data have no direct bearing upon the subjects with which this memoir is chiefly concerned, and would demand a much larger number of illustrations to make their arrangement intelligible than I dare ask for at present, I shall defer their publication until some other occasion.

An investigation such as this, which aims at explaining the salient features of the cerebrum in such a huge assemblage of animals as the Class Mammalia includes, must entail many obligations.

The unrivalled collection of mammalian brains in the Galleries and Stores of the Royal College of Surgeons were freely placed at my disposal by Professor Charles Stewart. To Dr. Henry Woodward, Dr. Charles W. Andrews, and Mr. Oldfield Thomas, I am indebted for the opportunity of examining the large collections of mammalian crania in the British Museum. Mr. W. L. H. Duckworth, in Cambridge, also freely permitted me to make use of the considerable collection of mammalian brains in his possession.

For valuable gifts of material for comparative purposes, I am under the greatest obligations to Professor Howes, the late Mr. Martin Woodward, Professors Wilson and Baldwin Spencer and Mr. James P. Hill (Australia), Dr. Robert Brown (South Africa), Dr. Charles Hose (Borneo), and especially Captain Stanley Flower (Egypt), among many others. Without the rich (and I believe unprecedented) collection of representative mammalian brains which I have thus been able to study, this communication would have lost its only claim to consideration, *i.e.* that it truly sets forth the tendencies of brain-evolution in the whole Mammalia, and not only in one small circumscribed group.

For the facilities which have been so generously afforded me in the accomplishment of this work I must express my great sense of indebtedness to all the gentlemen who have assisted me.

#### THE CEREBRAL HEMISPHERE IN THE GENUS LEMUR.

It is not necessary to describe the general form of the brain in the various genera of Lemuroidea, because the bulk of the literature quoted above deals with this subject, and certain of them, such as that of Gervais, are concerned exclusively with the shape of the brain. Moreover, all the important features of the brain-form will be discussed incidentally in these notes along with those peculiarities which are causally related to the modifications in shape.

When the dorsal surface of the brain of a *Lemur* is exposed by removing the roof of the cranium, little else than the cerebral hemispheres can be seen. In front of the pointed anterior pole of each hemisphere, the exposed area of the olfactory bulb projects very slightly more than one millimetre: and behind the broader, somewhat spatulate caudal extremities of the hemispheres in most cases only a very narrow band of the cerebellum is exposed as a series of seven rounded knobs fringing the margins of the hemispheres (fig. 1). So that in order to study the relationships of the constituent parts of the brain, it is necessary to turn to the examination of the ventral surface (fig. 4). In front there is the broad flattened olfactory bulb, about 11 mm. long and



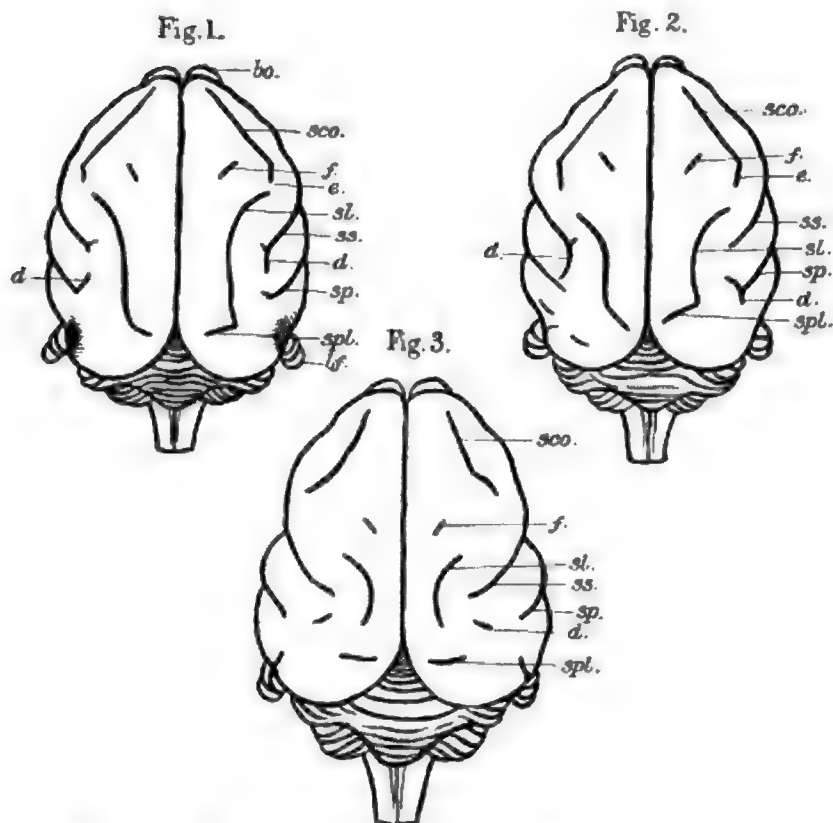


Fig. 1.—*Lemur macaco*. The dorsal aspect of the brain. Nat. size.

Fig. 2.—*Lemur fulvus*. The dorsal aspect of the brain. Nat. size.

Fig. 3.—*Lemur varius*. The dorsal aspect of the brain. Nat. size.

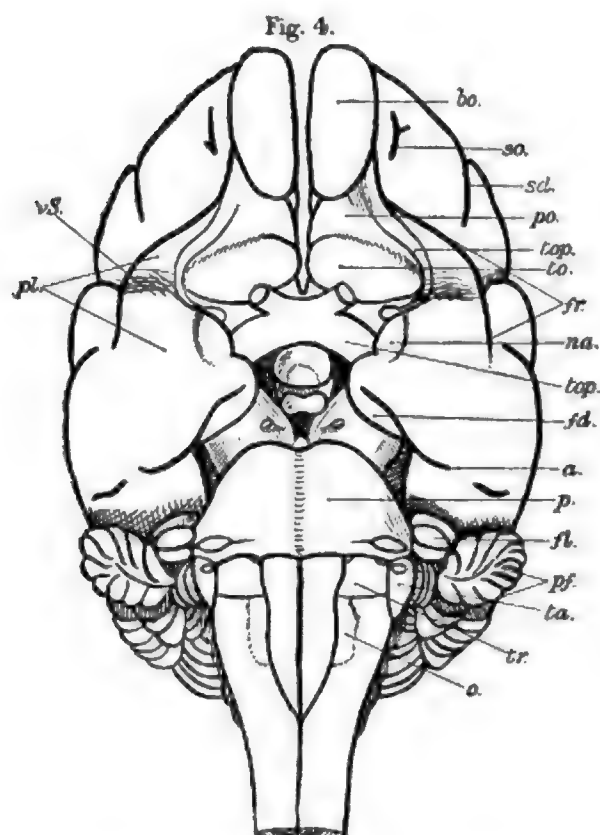
NOTE.—The differences in the shape and the extent of cerebral overlap of the cerebellum in figs. 1, 2, and 3 are probably merely individual variations and have no specific value.

For the significance of the reference-letters see below; the meaning of the letters *d*, *e*, and *f* is explained in the text\*.

\* LIST OF REFERENCE-LETTERS IN THE DIAGRAMS.

Sulcus ansatus— <i>an</i> .	Sulcus pseudosylvius— <i>sps</i> .
„ calcarinus— <i>ac</i> .	„ rectus— <i>sr</i> .
„ centralis— <i>scc</i> .	„ retrocalcarinus— <i>ars</i> .
„ coronalis— <i>sco</i> .	„ suprasylvius— <i>ss</i> .
„ cruciatus— <i>scr</i> .	Fissura hippocampi— <i>fh</i> .
„ diagonalis— <i>scl</i> .	„ rhinalis— <i>fr</i> .
„ ectosylvius anterior— <i>sea</i> .	„ prima— <i>fp</i> .
„ „ posterior— <i>sep</i> .	„ secunda— <i>fs</i> .
„ genualis— <i>sg</i> .	Bulbus olfactorius— <i>bo</i> .
„ intercalaris— <i>si</i> .	Calcar avis— <i>cal</i> .
„ lateralis— <i>sl</i> .	Cerebellum— <i>c</i> .
„ orbitalis— <i>so</i> .	Clastrum— <i>cl</i> .
„ paracalcarinus— <i>spc</i> .	Commissura anterior— <i>ca</i> .
„ postlateralis— <i>spl</i> .	Copula pyramidale— <i>cop</i> .
„ postsylvius— <i>sp</i> .	Corpus callosum— <i>cc</i> .





*Lemur fulvus*.—The ventral aspect of the brain.  $\times 2$ .

Corpus striatum—*cs*.  
 Corpora quadrigemina—*cy*.  
 Anterior pair of corpora quadrigemina—*cqa*.  
 Posterior " " —*cqp*.  
 Corpus geniculatum ant. (laterale)—*cya*.  
 " " post. (mediale)—*cyp*.  
 Fascia dentata—*fd*.  
 Floculus—*fl*.  
 Fornix—*for*.  
 Hippocampus—*h*.  
 Insula—*ins*.  
 Lobus flocculi—*lf*.  
 " anterior—*la*.  
 " medius—*lm*.  
 " pyriformis—*lp*.  
 Nodus—*no*.

Nucleus amygdala—*na*.  
 Olive—*o*.  
 Parafloculus—*pf*.  
 Pons—*p*.  
 Pedunculus olfactorius—*po*.  
 Psalterium—*ps*.  
 Pyramid (bulbar)—*py*.  
 " (cerebellar)—*pyr*.  
 Tractus olfactorius—*tol*.  
 " opticus—*top*.  
 Trapezium—*tr*.  
 Tuberculum hippocampi—*th*.  
 " olfactorium—*to*.  
 " acusticum—*ta*.  
 Uvula—*uv*.  
 Vallocula Sylvii—*vs*.

*Other individual references are explained in the text.*

The name "retrocalcarine" has been substituted for "postcalcarine" throughout, the latter having been already employed in another sense by other writers.

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about half as broad, lying in contact with the under surface of the cerebral hemisphere except in the anterior 1.5 mm. of its extent\*.

Its posterior end is joined to a flattened peduncle which is as broad as the bulb itself. It is very short, for it pursues a course of only 3 or 4 mm. before it becomes attached to the base of the cerebral hemisphere. In this respect it differs most decidedly from the very long and attenuated olfactory peduncle of the Apes; but, on the other hand, a short thick peduncle like that of the Lemur is found in the vast majority of mammals, and must be regarded as the common mammalian type.

The lateral half of the peduncle is covered by a dense thick bundle of fibres which constitutes the tractus olfactorius [lateralis]. This white covering also extends over the lateral border of the peduncle. The internal half of the ventral surface and the mesial border present a greyish appearance, because the medullary fibres of the so-called mesial tract are much less numerous and more scattered than those of the lateral tract. In the elongated peduncle of all Monkeys the whole peduncle appears to consist of nerve-fibres, so that its real constitution is not so obvious as it is in the Lemurs.

Just behind the insertion of the olfactory peduncle into the base of the hemisphere there is a transversely-placed, oval, puckered area of grey substance, 4 mm. broad and about 2.5 mm. in the sagittal direction. This is the tuberculum olfactorium—a peculiar cortical formation coating the ventral surface of the head of the corpus striatum. The features of this body are exceedingly constant throughout the Mammalia, but become somewhat obscured in the adult brain of Man and the Anthropoid Apes. The mesial surface of the olfactory peduncle extends on to the corresponding surface of the hemisphere just in front of the tuberculum olfactorium.

The lateral wall of the olfactory peduncle is prolonged backward into continuity with the pyriform lobe. The latter begins in front as a narrow horizontally placed grey band 3 mm. wide, the internal part of which is covered by the (external) olfactory tract. Opposite the outer extremity of the tuberculum olfactorium it becomes bent at right angles upon itself (fig. 6) and at the same time broadens to almost four times the width, so that its posterior part forms a very prominent rounded boss projecting 4 mm. below the level of the ventral surface of the anterior part. The transverse depression formed by this sudden bend is the vallecule Sylvii—a furrow which is quite distinct from the fossa and fissura Sylvii.

The vallecule Sylvii is much deeper and more pronounced in the Lemur than in most mammalian brains of other orders. In some of the smaller New-World Apes, such as the Hapalidæ, the vallecule presents features exactly analogous to that just described, the posterior part of the pyriform lobe being bent at an angle of 90° on the anterior part; but in most Apes the angle of bending becomes much more acute, the posterior part bulges forward over the anterior part of the pyriform lobe; and the vallecule Sylvii becomes a very deep cleft, which is commonly regarded as part of the stem of the true Sylvian fissure.

\* These measurements refer to a fresh specimen of *Lemur fulvus*, and may be regarded as a fair average of all the specimens of the genus *Lemur* which I have examined.

At the antero-mesial aspect of the natiform eminence (as the posterior part of the pyriform lobe is often called) there is an elliptical area bounded laterally by a shallow groove. Retzius has called this the "gyrus lunaris" and has shown how remarkably constant it is in the Mammalia\*. I am not aware that anyone has ever considered the significance of this little body (which I have studied not only in most Mammals, but also in the Reptilia); its nature is at once revealed in the Lemur's brain by a section at right angles to its long axis. It is clearly nothing else than the surface of the nucleus amygdalæ and is not therefore strictly a part of the pyriform lobe.

At the mesial border of the pyriform lobe we find a peculiar depressed grey band, which is erroneously labelled "gyrus uncinatus" by Flatau and Jacobsohn†. It is merely the lower end of the fascia dentata, whereas the uncinate gyrus is represented by the pyriform lobe itself. These writers adopt a very unusual and utterly misleading nomenclature when they call the anterior part of the pyriform lobe by the name "gyrus hippocampi" (p. 195).

In most Lemurs the rhinal fissure, which is the lateral boundary of the pyriform lobe, becomes almost wholly obliterated. This also happens in such Chiroptera as *Pteropus* and *Cynonycteris*. I have, however, been fortunate enough to obtain the brain of a *Lemur fulvus*, in which the rhinal fissure is retained in a form as distinct as it is in most mammals (figs. 4 and 6). I have also in my possession another brain of the same genus in which the whole of the rhinal fissure is visible, although it is very shallow; and also the cranial cast of yet another in which it is quite distinct. These three examples are, however, exceptional.

The fissure is distinctly visible upon the lateral aspect of the first-mentioned brain (fig. 6) pursuing a course (from the cleft between the olfactory bulb and the hemisphere) backward with a very slight upward inclination. Just behind the vallecule Sylvii it suddenly bends downward at an obtuse angle and curves horizontally backward to a point midway between the vallecule Sylvii and the posterior margin of the hemisphere. Behind this point there is no line of demarcation between the pyriform lobe and the neopallium.

In Monkeys no part of the rhinal fissure is visible upon the lateral aspect of the hemisphere: the relatively greater size of the neopallium and the much smaller absolute dimensions of the pyriform lobe shift it wholly on to the ventral, or even mesial, surface.

In the brain of most members of the genus *Lemur*, all that remains to represent the rhinal fissure is the angle and often only the posterior limb of the angle (fig. 7). In such cases, however, a careful examination enables one to distinguish the pyriform lobe from the neopallium, and thus determine the situation from which the fissure has been obliterated.

The olfactory tract (fig. 4) ends in the vallecule Sylvii in a distinct "tubercle of the

\* Gustav Retzius, "Windungen des Rhinencephalons," Biolog. Untera., N. F. viii. p. 2 (1898). The condition which he represents in the Rodent *Dasyprocta*, Taf. 7. fig. 10, closely resembles that of the *Lemur*.

† Handb. d. Anat. u. vergleich. Anat., Berlin, 1899, Taf. 5. fig. 2.



approximately vertically from the patch of fascia dentata on the ventral surface to the posterior end, or splenium, of the corpus callosum.

In the greater part of its extent this hippocampal formation conforms to the plan which we may call characteristically mammalian (such as we find, for instance, in the brain of *Tamandua* [*vide* the "Brain in the Edentata," *op. cit. supra*, figs. 10 & 23, p. 317]). There is, as in *Tamandua*, a well-defined sub-splenic flexure, and the wrinkled band of fascia dentata curves around on the under surface of the corpus callosum in the characteristic manner and then tapers as it merges in the circumcallosal hippocampal vestiges. A little hemispherical area of "hippocampus nudus" fills up the concavity of the arc formed by the sub-splenic bending of the fascia dentata, just as I have represented it in *Tamandua* (*op. cit.* p. 320, fig. 23). In all of these respects the hippocampal formation conforms to the typical mammalian condition, which I have described in detail in the above-quoted work.

In a recent memoir Zuckerkandl has briefly referred to the "hippocampus nudus" (his "Balkenwindung") in the Lemurs\*. He describes it as being "zapfenförmige" in *Lemur catta*, *L. varius*, *L. mongoz*, and *L. coronatus*, and "kurze zapfenförmige" in *Chiromys*.

The lower extremity of the hippocampal formation presents a peculiar modification not found in most mammals. Several years ago I called attention to the peculiar fact that a part of the hippocampus is rolled in such a manner that it becomes completely inverted: the surface which was originally deep is then superficial, and *vice versa* (Journ. of Anat. and Phys. vol. xxxii. p. 28). A strip of this "inverted hippocampus" separates the fascia dentata from the fimbria in the Lemur, as also happens in most mammals; but this becomes greatly expanded at its lower extremity to form a "hippocampal tubercle," such as is found in *Orycteropus* ("The Brain in the Edentata," *op. cit.* fig. 23, p. 315). A hippocampal tubercle of similar constitution occurs in all the Apes, and has been accurately described in the human brain by Giacomini and Retzius (compare Journ. Anat. and Phys. vol. xxxii. pp. 28 & 29).

In the Prosimian brain the tubercle varies considerably in size and prominence, and in the brain of *Nycticebus* practically vanishes; it is never so prominent as it is in the Apes, although its constitution is the same. In some Insectivores, such as *Macroscelides*, I have seen a condition closely resembling that of the Lemurs, and have also seen instances of the same phenomenon in *Orycteropus* and in the brain of a Manatee. This peculiar condition is apparently inherited by all the Primates, both Lemurs and Apes, from some primitive Insectivore-like ancestor, which has also transmitted it to the primitive Aard-vark and that peculiar Eocene stock which has persisted with little change as the Sirenia.

The corpus callosum is very long and has a very plump caudal extremity or splenium, and a very thick and fully-recurved genu. As a whole, it closely resembles that of the Platyrrhine Apes. The greatly attenuated psalterium, or hippocampal commissure, resembles the common mammalian type, such as is found, for example, in

\* E. Zuckerkandl, "Beitr. zur Anat. des Reichcentrums," Sitzungsab. Akad. Wiss. Wien, Math.-nat. Cl., Bd. cix, Abth. iii. 1900.

*Tamandua*, *Felis*, or *Ovis*. It is, however, hardly so plump as in any of these mammals, and yet it is not nearly so small and attenuated as that of the Apes. In the Hapalidæ, for example, the psalterium becomes so extremely reduced (*vide* Journ. of Anat. and Phys. vol. xxxii. fig. 23, p. 51) that Beever failed to find it even by histological means. In the Lemurs its size is more considerable, and the chief accumulation of its fibres is never wholly separated from the splenium by an interval devoid of commissural fibres, as happens in *Midas* (*op. cit.*) and the other Hapalidæ.

The septum lucidum, precommissural area, and anterior commissure present the usual relations.

Immediately behind the hippocampal tubercle there is a very deep indentation, which may possibly represent the caudal remnant of the rhinal fissure (fig. 5, *a*). It begins close to (but without actually joining) the hippocampal fissure and passes obliquely downward and backward. On the base of the brain (fig. 4) it has all the appearance of joining the hippocampal fissure. Its extent and direction vary considerably in different brains of even the same species. In many cases (as, for instance, fig. 5) its dorsal lip projects downward as a prominent rounded knob overlapping the deepened notch.

Upon the mesial surface of the hemisphere there are a number of very stable and constant sulci, and usually some other more variable furrows.

By far the most important of these is a group of three, which may be called the calcarine complex. This is a triradiate pattern of sulci situated behind the splenium of the corpus callosum; the ventral limb may be distinguished as "calcarine," the caudal as "retrocalcarine," and the dorsal as "paracalcarine."

Above and parallel to the corpus callosum there is a sulcus which will be called "intercalary"; and in front of the genu there is generally a "genua sulcus"\* of Krueg (fig. 5).

There is always an oblique sulcus placed below the retrocalcarine sulcus, which for the present may be referred to simply as *b*.

There is also a very oblique sulcus (*c*) on the caudal margin of the hemisphere, midway between the furrows *a* and *b*.

That portion of the mesial surface of the cerebral hemisphere which lies below and behind the corpus callosum is adapted to the shape of the contiguous structures. A deep depression receives the optic thalami, a much smaller and shallower depression below and behind the splenium is produced by the quadrigeminal bodies, and the broad flattened area behind it is so moulded by contact with the upper surface of the cerebellum.

The calcarine sulcus begins inferiorly within the deep thalamic fossa just above the sulcus *a*; it ascends for about 3 mm. parallel to the hippocampal fissure and then bending backward it crosses the rim of the thalamic fossa, traverses the mesencephalic fossa, and ends in the cerebellar area, about 3 mm. behind the splenium. It attains a depth of 6 mm. in its posterior part.

In every brain (with only one exception) belonging to the genus *Lemur* which I have examined the calcarine sulcus was continuous with the retrocalcarine sulcus, the two

\* It is not altogether certain whether it may not represent the "rostral" sulcus.



furrows uniting at an angle of  $120^\circ$ . The retrocalcarine sulcus is confined to the cerebellar area. It passes backward with a very slight upward inclination for a distance of 8 mm. The degree of obliquity of this sulcus shows considerable variability. In some cases it is almost horizontal; in others it is removed as much as  $30^\circ$  from that plane. At its meeting place with the calcarine sulcus it is as deep as the latter.

The paracalcarine sulcus passes obliquely upward and forward from the angle of junction of the other two sulci almost as far as (in rare cases even actually crossing) the dorsal margin. In some cases its terminal piece is bent vertically upward. This sulcus is generally shallower than the calcarine, so that it appears to cut deeply into the upper lips of (without actually joining) the sulcus formed by the junction of the calcarine and the retrocalcarine furrows. In one case, however, I have seen the calcarine and paracalcarine sulci joined, the retrocalcarine being the separate element. This is instructive, because it shows that the retrocalcarine sulcus possesses a certain amount of individuality and is not a mere mechanically-produced extension of the calcarine sulcus. The sulcus *b* varies considerably in length and depth in different brains. In the large brain of a *Lemur varius* I have seen it represented by a very faintly marked depression less than 3 mm. long. In other cases it is a furrow 8 mm. long and 2 or even 3 mm. deep. It undoubtedly represents the most caudal element of that composite sulcus of the human brain known as the "collateral."

The sulcus *c* is even more variable. It may be a mere pit in the depression caused by the roof of the bony capsule of the floccular appendage (so-called "petrosal" lobule) of the cerebellum, or it may become a deep sulcus 5 or 6 mm. long.

On the external aspect of the neopallium the sulci are no less variable (figs. 6 & 7). The deepest and most constant furrow is that which is commonly called the Sylvian fissure. It really consists of an *apparent* blending of two *actually separate* overlapping sulci. One of these, which I shall call pseudosylvian, proceeds vertically upward (for a distance of 4 mm.) from the bend (or more strictly from the posterior limb) of the rhinal fissure. It appears to (but does not actually) join a second sulcus, which is obliquely placed, so that the two sulci form an angle of about  $150^\circ$ . This upper oblique sulcus I shall call the "suprasylvian."

If the lips of these sulci be separated, it will be found that the sulcus pseudosylvius cuts deeply backward into the hemisphere, so that its posterior lip forms an operculum (4 mm. long and almost equally thick) which overlaps a depressed area (fig. 6*a*). The lower part of the sulcus suprasylvius overlaps the s. pseudosylvius (fig. 6), and the anterior lip of this part of the furrow is also slightly operculated. Hence there is an area (about 6 mm. long and 1 mm. high) submerged and hidden from view by the anterior opercular lip of the suprasylvian and the posterior opercular lip of the pseudosylvian sulci (fig. 6*a*). The few observers who have in any way referred to this depressed area regard it as the insula Reilii. Holl (*op. cit. supra*) regards it as the submerged homologue of Leuret's first arcuate gyrus of the Carnivora. The degree of accuracy of these statements will be discussed below.

Between the upper end of the suprasylvian sulcus and the dorso-mesial edge of the hemisphere there is a sagittal sulcus of very variable length, which may be distinguished



by the name "lateral." The anterior extremity of this sulcus always bends laterally, so as to be approximately parallel to the upper part of the suprasylvian sulcus (fig. 1). Its posterior extremity usually becomes bent in a mesial direction. It often happens, however, that this mesially directed limb remains as a transverse sulcus widely separated from the sulcus lateralis (fig. 3). It may be distinguished as the postlateral sulcus.

Behind and parallel to the suprasylvian and pseudosylvian sulci there is a sulcus of varying length and depth, which may be distinguished as postsylvian.

The mode of termination of the supra- and postsylvian sulci is exceedingly variable (compare figs. 1, 2, 3, 6, and 7). In many cases the upper extremity of the suprasylvian sulcus bends backward so as to almost reach the postsylvian (fig. 6): in other cases (fig. 7) the latter curves forward to approach the suprasylvian; and in other cases again (fig. 3) the intercalated furrow is separated from both sulci. We may distinguish it by the letter *d*, and defer the discussion of its significance until later.

From a point about 5 mm. in front of the middle of the suprasylvian sulcus a furrow (which may attain a length of 20 mm.) passes obliquely forward and inward to end upon the anterior pole of the hemisphere. For reasons which will be discussed later, I shall distinguish this sulcus by the not-obviously appropriate name "coronalis." In almost all cases the posterior part of this furrow is bent backward and inward toward the lateral sulcus (fig. 2). We may distinguish this little fragment from the rest of the sulcus by the letter *e*.

Midway between this sulcus and the mesial border there is a very short furrow, the direction of which is by no means constant. In most cases, however, it is directed laterally and forward. For the present I shall call it the "sulcus *f*."

Upon the orbital surface of the hemisphere there is a small sulcus of very variable size, depth, and shape alongside the olfactory bulb. It is the orbital sulcus. In some brains it is either quite absent or represented only by a very shallow depression.

Immediately in front of the lower extremity of the suprasylvian sulcus (which is generally exposed in the genus *Lemur*) there is often a small oblique sulcus in the orbital margin. This I shall call "diagonal."

Near the floccular notch (in the caudal margin of the hemisphere) there is generally a small oblique sulcus, which may or may not extend into the floccular depression and overlap the sulcus *c*. It may be distinguished for the present by the letter *g*.

[In the foregoing enumeration of these sulci I have deliberately used terms which no other writer has employed in reference to the Lemur's brain, not only to avoid the hopeless confusion which the varied nomenclature of Beddard, Ziehen, Chudzinski, and Flatau and Jacobsohn would entail, but also for morphological reasons, which will appear later and, I believe, justify this course of action.]

In different individuals of the genus *Lemur* the cerebral hemisphere exhibits slight variations in size, shape, and the arrangement of its sulci.

The only writer, so far as I can remember\*, who has even so much as hinted at the

\* As most of the literature is not at present available, I am unable to consult the memoirs of Gervais in regard to this point; but, unless my memory belies me, this statement is correct.

possibility of these differences having any specific value is Beddard \*. His remark that "the bigger brains are on the whole more complex than the smaller" may seem a mere truism; but I have found some noteworthy exceptions to it. Thus one of the simplest Lemur's brains I have seen was also by far the biggest: it belonged to a *Lemur varius* and weighed 39 grammes, its cerebral hemispheres being each 49 mm. long and 21.5 mm. broad; it had no fronto-orbital sulci, very poorly developed orbital and collateral sulci, and unusually short lateral, parallel, and straight sulci (fig. 3).

My examination of crania bears out the statement of Beddard that the variety *anjuanensis* has the simplest brain of all members of the genus. It is the only brain in which no trace of the sulcus *f* is found. But with this (possible) exception, all of Beddard's remarks on supposed specific characters are the mere record of individual variations, every one of which may occur in any species.

So far as my observations go, it is quite impossible to assign any specific value to the variations. But this may possibly be due to the fact that an insufficiently large number of brains was available for examination. As the variations are practically wholly confined to the external aspect of the hemisphere, the investigation necessary to settle this question can most readily be carried out on a series of skulls, from which we can readily determine the size, shape, and pattern of the sulci in the cerebral hemisphere.

Concerning the exact size and shape—*i. e.* chiefly the amount of cerebellum overlapped—there are only very scanty data.

Max Weber records the brain-weights of two specimens of *Lemur varius*, Geoff.: that of a male 33 grms., being  $\frac{1}{6\frac{1}{3}}$  of the body-weight, and that of a female 28.7 grms., being  $\frac{1}{7\frac{1}{5}}$  of the body-weight. A representative of this species died in the Ghizeh Zoological Gardens, and I found its brain-weight to be 39 grms. and its body-weight 2900 grms., *i. e.* the brain was  $\frac{1}{7\frac{1}{4}}$  of the body-weight.

Max Weber also records the weight of the brain and its relation to the body-weight in two females of *Lemur mongoz*, L., as 28 ( $\frac{1}{7\frac{1}{6}}$ ) and 21.1 ( $\frac{1}{6\frac{1}{6}}$ ) respectively. The only other records of brain-weights by Ziehen, Flatau and Jacobsohn, are of little value, because they refer to specimens the weights of which were altered by the action of reagents. I have found that the extent of the area of cerebellum uncovered by the cerebral hemisphere is subject to variation. It was largest in a brain of *Lemur varius* (fig. 3), but, as I have found the extreme types of variation in the brains of two specimens of *Lemur fulvus* (which died in the same week and were examined under exactly similar conditions), it does not seem possible to attach any specific importance to this fact. (Compare figures 6 and 7, also figures 1, 2, and 3.)

With regard to the variations in the measurements of the hemispheres, my data are very scanty.

Flatau and Jacobsohn give the following measurements for a specimen of *Lemur macaco* (*op. cit.* p. 174):—

Maximum length of cerebral hemisphere 48 mm.

Greatest breadth of cerebrum 38 mm.

Greatest height of hemisphere 28 mm.

\* "On the Brain in the Lemurs," *Proc. Zool. Soc.* 1895, p. 143.

These measurements are extraordinarily large when it is considered that the brain weighed only 26.3 grms., after being in 10 per cent. formol solution for eight days.

The corresponding measurements in an adult female *L. macaco* I found to be 13 mm., 37 mm., and 26 mm. respectively. These measurements (which were checked by comparison with the cranium) indicate a brain-shape very different to that of Flatau and Jacobsohn's specimen. If the latter were swollen as the result of the formalin, the value of the elaborate tables of measurements in their book is seriously discounted.

The hemispheres of a *Lemur fulvus* were 46 mm. long and 38 mm. broad; and the corresponding measurements in a *Lemur varius* were 49 mm. and 43 mm. respectively.

The size of the brain of the extinct *Lemur Julliyi* greatly exceeded that of any of the recent Lemurs; for its cerebral hemispheres were 59 mm. long, 48 mm. broad, and 31 mm. deep.

Turning to the consideration of the cerebral sulci and fissures, a considerable amount of variation is found.

The rhinal fissure usually becomes aborted, with the exception of a very small furrow near the olfactory peduncle and the *apparent* recurved inferior extremity of the pseudosylvian sulcus. In the specimen of *Lemur fulvus* described above, the greater part of the fissure persisted. In another specimen of *L. fulvus*, and in one each of *L. macaco* and *L. varius*, I have seen a faintly marked furrow representing the whole fissure.

The two brains of *L. varius* (one in the College of Surgeons and one from Ghizeh) agree in the following respects:—The diagonal sulcus is absent; the orbital sulcus is so poorly developed as to be a mere insignificant depression; the lateral sulcus is a simple regular arc, widely separated from the postlateral and coronal sulci; the sulcus *d* is not joined to either the supra- or to the postsylvian sulcus; the collateral sulcus is very small and shallow; and, apart from the small floccular sulcus, there is no sulcus behind the postsylvian.

All of these features may be regarded as indicative of a tendency to simplicity, which is all the more significant in that the brain in this species is appreciably larger than that of most other members of the genus. It remains for future research to determine whether these features may be regarded as distinctive of the species *varius*.

I have examined two brains of *Lemur macaco* and several cranial casts. In addition Flatau and Jacobsohn (*op. cit.*) have given a full description of a brain of this species.

The diagonal and orbital sulci are constantly present, but the latter shows a tendency to become irregular by the development of a lateral ramus. Sometimes also its direction varies. The mode of ending of the upper extremities of the supra- and postsylvian sulci is variable. In most cases the upper extremity of the suprasylvian sulcus is simple; but Flatau and Jacobsohn represent (Taf. 3. fig. 1, 4) a small added horizontal sulcus. Generally the upper end of the parallel sulcus curves forward, representing a fusion with the sulcus *d*, which usually does not exist as a separate element in this species. Unlike the condition found in *L. varius*, there is no distinct postlateral sulcus, but there is a very oblique furrow, united at a very obtuse angle with the caudal end of the lateral sulcus.

I have never seen the sulcus described as "*temporalis secundus* (oberer Teil)" by

Flatau and Jacobsohn in the brain of *Lemur varius*: nor have I ever found the sulcus labelled "Nebenfurche" (Taf. 3. fig. 2, 2) in the brain of any Lemur.

In the brain of *Lemur fulvus* the diagonal sulcus is generally well-developed and often deeply notches the supraorbital margin.

The lateral and coronal sulci approach much more closely than is the case in the other species, and in some instances they even seem to join. Thus Beddard says (Proc. Zool. Soc. 1895, p. 143):—"In the brain of *Lemur mongoz* the angular [lateral and infero-frontal] sulci are completely continuous." But even if this sometimes happens, it is by no means the usual condition in *L. fulvus*. For, as the same writer remarks (p. 143), this does not occur in *L. albifrons*, nor in *L. nigrifrons* nor *L. anjuanensis*, all of which may be included in the species *fulvus*. Within this species all varieties of the upper ends of the supra- and postsylvian sulci are found. Sometimes a long arcuate sulcus *d* is fused at one end to the suprasylvian sulcus and almost joins the postsylvian at the other. Not infrequently the sulcus *d* is joined to the postsylvian and not to the suprasylvian; but in some cases it remains independent of both, as in the species *varius*.

In most cases the caudal end of the lateral sulcus behaves as it does in the species *macaco*, and not as in *varius*.

In the two specimens of *Lemur catta* which I examined there was nothing distinctive and they might well have belonged to the species *fulvus*.

The skull of *Lemur rubriventer*, Geoff., exhibits ridges corresponding to typical suprasylvian, postsylvian, lateral, postlateral, coronal, orbital, and diagonal sulci, with nothing indicative of a distinct specific type.

The large brain of the extinct *Lemur Jullii* (*Palæchirogaleus Jullii*, G. Grand.) exhibits the typical Lemurid plan of sulci with diagrammatic clearness.

The suprasylvian sulcus with a long deeply-incised inferior exposed limb, the shallower furrow indicating the pseudosylvian sulcus; simple, long, linear orbital and diagonal sulci; lateral and coronal sulci which almost (if not quite) meet as in *Lemur fulvus*; and a small sulcus *f*, all conform to the most typical Lemurid pattern.

The orbital sulcus presents none of the irregularity which it has acquired in most of the recent Lemurs.

#### THE CEREBRAL HEMISPHERE IN THE GENUS HAPALEMUR.

An examination of the ridges on the interior of the cranial cavity of *Hapalemur* reveals a pattern of sulci which does not appreciably differ from that exhibited in the genus *Lemur*. The typical Sylvian fissure, a short lateral sulcus, a long coronal sulcus, and a typical linear orbital sulcus are present.

Milne-Edwards has published illustrations of a brain of *Hapalemur simus*\* which presents similar features. Beddard has described three brains belonging to this genus, two of the species *griseus* and one of the species *simus*†. The hemispheres of the smaller specimen of the former species were 33 mm. long and 26 mm. broad, the larger

\* 'Histoire de Madagascar,' (2) tome vi. pl. 122\*. figs. 1, 2, 3, 4, and 5.

† Proc. Zool. Soc. 1901, pp. 127 & 128; also Proc. Zool. Soc. 1891, p. 457.

being 35 mm. long and 28 mm. broad: the corresponding measurements in the species *simus* were 40 mm. and 31 mm. respectively. The brain of *Hapalemur* therefore is considerably smaller than the average size in *Lemur*.

In the brain of *Hapalemur simus* (Proc. Zool. Soc. 1901, p. 127, text-fig. 24) the upper end of the suprasylvian sulcus is bifid; but it is not fused to a long sulcus *d*, as is the case in Beddard's first specimen of the genus, *griseus* (*ibid.* p. 128, text-fig. 25). There is a typical coronal sulcus in both species, bent in exactly the same manner as so often happens in the genus *Lemur*. Lateral, orbital, parallel, and even diagonal sulci and the furrow *f* occur exactly as in the genus *Lemur*.

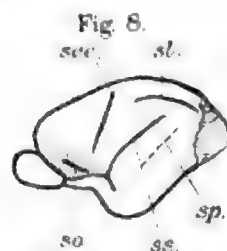
It is clear that the brain of *Hapalemur* is, to all intents, identical with that of *Lemur*; and the features which Beddard thinks may possibly amount to specific characters can be nothing else than variations such as we find in almost every species of *Lemur*.

H. O. Forbes states\* that "the brain [in the genus *Hapalemur*] is narrower and shallower than that of the genus *Lemur*, and presents no specially close resemblance to the same organ in the *Indrisinae* or the *Lorisinae*." With the latter part of this quotation I quite agree; and if the former part is also true, it indicates, in comparison with *Lemur's* brain, a slightly nearer approach to the pithecoïd type.

#### THE CEREBRAL HEMISPHERE IN THE GENUS *LEPIDOLEMUR*.

The olfactory bulb appears to project beyond the hemisphere as it does in the *Lorisinae*, the *Galaginae*, and in *Tarsius*.

The pattern of sulci which a study of the cranial ridges in a series of skulls has shown to exist in *Lepidolemur* differs in many respects from the arrangement which is common to the genera *Lemur* and *Hapalemur*.



*Lepidolemur mustelinus*.

Lateral aspect of the cranial cast of the left cerebral hemisphere. Nat. size.

In a skull of *Lepidolemur mustelinus* in the British Museum there are typical simple linear Sylvian, lateral, orbital, and a very shallow postlateral sulcus, and another sulcus apparently representing the conjoint elements *e* and *f*, such as often happens in *Pro-pithecus* and *Perodicticus*. This specimen also closely resembles that of one of the specimens of *Arahis* which I examined, the protruding olfactory bulbs constituting a small and relatively unimportant difference.

A second skull of the same species exhibited a pattern of sulci exactly similar to this,

\* "Monkeys," vol. i. (Allen's Naturalist's Library, 1893), p. 81.

except that no trace of a ridge corresponding to the postsylvian sulcus was present. There is neither a coronal nor a postlateral sulcus.

In a skull of *Lepidolemur leucopus* in the British Museum there is no trace of either the orbital, coronal, or postsylvian sulci, or of the furrows *e* and *f* in *Lemur*.

So far as I am aware, all that is known of the brain itself in this genus is represented by a series of not altogether satisfactory drawings (without any description of any kind, except the legend "brain of *Lepidolemur ruficaudatus*") in Milne-Edwards's work\*.

From an examination of the profile (fig. 1*b*), one might imagine that typical coronal and lateral sulci of the Lemurid type were present; but the appearance presented by the sketch of the dorsal surface (fig. 1) is so different that it is difficult to believe that it represents the same brain. As I had inferred from the examination of two of the three skulls, there is no postsylvian sulcus.

These drawings unfortunately give us little information of any value.

So far as I am able to judge from the crania which I have examined, the brain must present many features resembling those of the Indrisinæ and others (of less importance) like those of the Lorisinæ (especially *Perodicticus*) and Galaginæ.

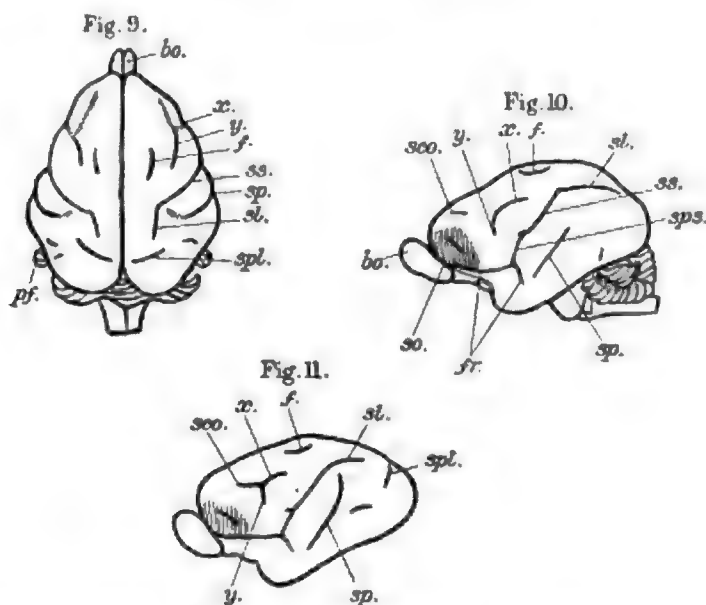


Fig. 9.—*Nycticebus tardigradus*. Dorsal aspect of a cranial cast. Nat. size.

Fig. 10.—*Nycticebus tardigradus*. Left aspect of a brain. Nat. size.

Fig. 11.—*Nycticebus tardigradus*. Lateral aspect of the left cerebral hemisphere of another brain. Nat. size.

#### THE BRAIN IN THE LORISINÆ.

It is convenient to consider *Nycticebus* first. The brain in this genus is not only smaller than that of *Lemur*, but also presents some noteworthy differences in shape.

The cerebral hemispheres of the only fresh specimen of *Nycticebus tardigradus* which I have seen are 34 mm. long, 28 mm. wide, 23 mm. high.

\* 'Histoire de Madagascar,' (2) tome vi. 43<sup>e</sup> fasc. 1897, pl. 273. figs. 1, 1*a*, 1*b*, 1*c*, and 1*d*.



If a vertical line be drawn from the most prominent part of the "natiform eminence" of the pyriform lobe, it will be found that more than half of the hemisphere lies behind the vertical line. This is not the case in *Lemur*, but is so in all Apes.

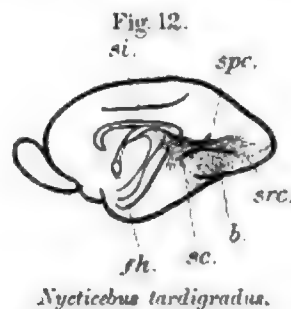
There is a more pronounced caudal extension of the hemisphere, so that the cerebellum is almost completely overlapped.

There is a much smaller "orbital area" in *Nycticebus* than in *Lemur*. In the latter it extends in the caudal direction as far as the pseudosylvian sulcus, whereas in the former it only extends to a point midway between the pseudosylvian sulcus and the anterior pole of the hemisphere.

In the genus *Lemur* the olfactory bulb is a horizontally flattened plate, the bulk of which is covered by the hemisphere. In the genus *Nycticebus* the bulb is a vertical sagittal plate, 5 mm. of the length (9 mm.) of which projects beyond the anterior pole of the hemisphere. It is only 1.5 mm. broad (*i. e.* transverse thickness).

The anterior rhinal fissure is not obliterated: of the posterior rhinal fissure only one or two millimetres exist as a furrow, but if a fresh brain be examined a very faint depression is visible extending horizontally backward with a slight downward bend. This can be traced on to the mesial surface.

The flexure of the pyriform lobe is slightly more acute and pithecoïd than that of *Lemur*, so that the vallecule Sylvii is more cleft-like. The other parts of the rhinencephalon closely resemble the corresponding regions in the genus *Lemur*, with the exception of the lower end of the hippocampus. For in *Nycticebus*, unlike every other Prosimian known to me, there is no well-defined hippocampal tubercle. The inverted hippocampus merely becomes slightly broader at its lower end, as it does in most mammals (fig. 12).



*Nycticebus tardigradus.*

Mesial aspect of the right cerebral hemisphere. Nat. size.

The corpus callosum is a very thin plate of fibres 12 mm. long; its anterior and posterior parts are not so markedly thickened as they are in *Lemur*. There is an exceptionally extensive arcuate genu.

The form and relations of the calcarine group of sulci are identical with those described in *Lemur*. The paracalcarine sulcus is, however, much shorter. The intercalary sulcus is relatively larger than it is in *Lemur*, and its posterior extremity is slightly bifid: the upper limb being the deeper faintly foreshadows the upturned posterior end of the calloso-marginal sulcus of the Anthropoidea. There is neither a genual nor a rostral sulcus.



The Sylvian fissure is composed of two separate sulci, pseudosylvian and suprasylvian, as in *Lemur*; but in this genus they both pursue the same direction and overlap so slightly that it requires the closest examination to detect the lower end of the suprasylvian sulcus. As the result there is no obvious depressed area, such as is found in *Lemur*, but its homologue is found in the anterior lip of the furrow in the region of the lower end of the suprasylvian sulcus. The lower part of the pseudosylvian sulcus is very shallow.

The upper extremity of the suprasylvian sulcus becomes directly continuous with the lateral sulcus, no submerged gyrus being found to separate the two elements.

The lateral sulcus bends backward, and then finally curves inward in a manner exactly analogous to that of *Lemur fulvus*.

There is a small bracket-shaped sulcus *f*, the concavity of which faces the middle line.

There is a sulcus about 7 mm. long in front of and parallel to the suprasylvian sulcus. Its upper part is bent backward so as to become almost horizontal. Thus the sulcus may be regarded as consisting of two limbs *x* and *y*. There is always a small sulcus just above the orbital margin which we may regard as the sulcus coronalis. In my type specimen this is so small as to be little else than a mere pit.

There is a simple linear postsylvian sulcus. In my specimen (fig. 10) there are no other sulci, nor even depressions to represent the sulci called *a*, *b*, *c*, and *g* in the brain of *Lemur*.

In the specimen of *Nycticebus tardigradus* [*Stenops javanicus*, Illig.] described by Flower (Trans. Zool. Soc. vol. v. pp. 103 *et seq.*) there are some slight differences. Thus the sulcus *y* appears to be absent and *x* is joined to the coronal sulcus, the resultant furrow being called "infero-frontal," which is the name Flower gives to the coronal sulcus of *Lemur*. The sulcus *f* is represented as a long sagittal furrow, which is called "supero-frontal" (p. 104). The writer remarks that the Sylvian fissure "makes a slight change in direction, continuing to extend backwards" (p. 104), but thinks that the lateral sulcus of the *Lemur* is absent.

He represents a well-developed postlateral sulcus, such as is not found in my specimen. Concerning this he says:—"A small sulcus running in a transverse direction on the upper surface of the hemisphere, at the junction of the parietal and occipital lobes, recalling the 'temporo-occipital' (*scissure perpendiculaire externe*) of the *Quadrumana*, which fissure is, however, wanting in the smaller American Apes, as in *Lemur*" (p. 104). We have seen above, however, that it sometimes occurs in *Lemur*, especially in the species *varius*; and even when absent as a separate element it is probably represented in the "tail" of the lateral sulcus, both in *Lemur* and *Nycticebus*.

In the specimen in the College of Surgeons Museum (fig. 11) the postlateral sulcus is a separate element on the left hemisphere, but is merged in the lateral sulcus on the right side.

The upper end of the postsylvian sulcus bends forward, as it does in many *Lemurs*. On the right hemisphere it presents an additional ramus parallel to the lateral sulcus. In both hemispheres there is a little sulcus behind the upper end of the postsylvian

sulcus. In an Ape's brain this would be called "inferior temporal." In this brain the sulci *x* and *y* appear to be joined to the coronal to form a triradiate pattern.

There is also a small collateral sulcus (fig. 12, *b*), such as the brain of *Lemur* presents.

Beddard says that "there appear to be more differences between the brain of [*Nycticebus tardigradus*] and that of its congener *Nycticebus javanicus* than between the different species of *Lemur* . . . the brain is more rounded in front, and the cerebellum more fully exposed than is indicated in Sir W. Flower's figure of *N. javanicus*. The angular fissure [Beddard thus refers to the sulcus designated *f* in my account and mistakes it for the 'lateral'] is short and instead of being straight it is crescentic . . the concavities facing each other. . . The infero-frontal [coronal] seems to be less conspicuous than in the other species of the genus and on one side of the brain it ran back to join the curved (anteriorly convex) presylvian fissure [the sulcus *x*], the homologue (?) of which latter in *N. javanicus* has a totally different direction. The parieto-occipital ('Simian') fissures [postlateral sulci] are better developed than in *N. javanicus* and reach the intercerebral sulcus" (Proc. Zool. Soc. 1895, p. 144).

The differences in shape which Beddard regards as specific features I have been unable to find upon examining a series of crania, and the features of the sulci upon which he lays stress are individual variations such as also occur in undoubted examples of the species *tardigradus*. So far as one can be guided by the evidence of cerebral anatomy, there is no reason for splitting up the species *tardigradus* to make another species (*javanicus*).

There can be little doubt that the brain which Chudzinski described under the title "*Loris gracilis*" (Bull. Soc. d'Anth. 1895, p. 436) is really that of *Nycticebus tardigradus*. It presents the arrangement of sulci typical of the latter; and this is very different from that of *Loris*. The Sylvian fissure is joined to the lateral in the typical manner, and the latter ends in a bifid extremity, which Chudzinski calls "portion externe de la scissure occipitale"; this is the postlateral sulcus.

The sulcus *f*, the postsylvian and the triradiate complex of the sulci *x*, *y*, and coronal resemble those described above in the specimen belonging to the College of Surgeons. There is a small sulcus behind the upper end of the postsylvian.

Ziehen based his account of the brain in this genus (Arch. f. Psych. xxviii. pp. 902-906) on four specimens (one of which is in the College of Surgeons, and another in the British Museum). He calls the mesially-bent extremity of the lateral sulcus the "Rudiment der Fissura parieto-occipitalis lateralis." [In respect to this sulcus the condition represented in his drawing resembles my type specimen.]

The sulci which I have labelled *f*, *x*, and *y* he regards as representatives of the sulcus centralis.

The sulcus behind the upper end of the postsylvian (his "temporalis superior") is called "temporalis inferior." Another small sulcus behind the lower part of the postsylvian, which I have not seen in any of my specimens, is regarded as the lower part of the same sulcus.

He represents a small separate furrow above the postsylvian, such as is often present in the Lemurs (*d*); and the connecting limb of the supra- and postsylvian sulci is also

shown. This he labels "Scheitelstück zu  $\theta$  [postsylvian]." On the mesial surface he represents, in addition to the calcarine group and the intercalary, a small rostral and two sulci labelled  $\beta'$  and  $\gamma$ . Of these,  $\beta'$  obviously represents the slight depression produced by the capsule of the floccular lobes, whereas  $\gamma$  represents the sulcus I have called "collateral" in *Lemur*.

Like Flower, he denies the presence of an *insula* (p. 906); but this arises from a misconception as to the nature of the region so-called. Both writers mean that a definite submerged area is not found in this genus.

Flatau and Jacobsohn repeat the curious error of Chudzinski and describe a brain, which can be none other than that of *Nycticebus tardigradus*, as being that of "*Stenops gracilis*." For not only does it exhibit the plan of sulci distinctive of *Nycticebus*, but its dimensions also are those of this genus and not those of *Loris* [*Stenops*]. If the brain which they describe really belongs to the genus *Loris*, we should have expected some comment from the authors as to its aberrant characters, which a comparison of the memoirs of Beddard and Ziehen ought to have demonstrated. [Moreover, a study of their account ('Handbuch,' last few lines on p. 194 and p. 195) might lead one to suppose that the authors do not clearly distinguish between the terms *Loris gracilis*, *Stenops gracilis*, *Stenops tardigradus*, *Stenops javanicus*, and *Nycticebus tardigradus*.]

The condition of their specimen differed from that of mine in possessing a separate postlateral sulcus and an inferior temporal. In these respects, as well as in the features of the mesial surface, it resembles the specimen in the College of Surgeons.

The sulci which Ziehen called "central" the above authors regard as "precentral." Otherwise they closely follow the teaching of the Utrecht psychologist.

They represent certain small furrows, which have not been mentioned above, such as those labelled "Spur eines Sulcus fronto-orbital" and "Fissura sublimbica posterior."

In addition to these records, I have examined two crania of this genus, and from one a plaster mould of the brain-cavity was made.

In one specimen (College of Surgeons, specimen 293, labelled "*Loris javanicus*") I found characteristic suprasylvio-lateral, postsylvian, and orbital sulci, the triradiate coronal  $+x+y$  complex, and the sulcus  $f$ . In addition there was a separate postlateral.

There seemed to be a diagonal sulcus between the sulcus  $x$  and the Sylvian complex, but of this I cannot be certain.

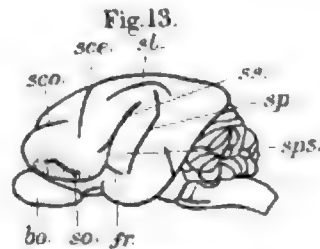
The other specimen, which was given me by Captain Stanley Flower, presented a pattern which differed from the last in the absence of any trace of a diagonal sulcus; it also possessed modifications of the upper ends of the postsylvian sulci in the two hemispheres exactly analogous to those found in the respective hemispheres of the brain in the College of Surgeons. Thus the upper end of the sulcus was bent forward on the left hemisphere; but bifurcated, and its chief branch bent back on the right side. There is also an inferior temporal sulcus.

It is interesting to note in these two casts that there is a definite postlateral sulcus in all four hemispheres, and in none of them is the caudal extremity of the lateral sulcus bent inward, as is invariably the case when the separate postlateral sulcus is absent. A comparison of the brain-case of my type specimen with the other cranium from Ghizeh

shows that the separate postlateral sulcus occupies the same position in regard to the skull as the mesially bent end of the lateral sulcus of the other specimen.

The brain of *Perodicticus* presents some very interesting features.

The olfactory parts of the brain resemble the corresponding regions in *Nycticebus*. The rhinal fissure resembles that already described in the latter genus.



*Perodicticus potto.*

Left lateral aspect of the brain. Nat. size.

The "Sylvian fissure" is composed of the pseudosylvian and suprasylvian sulci as in *Lemur*, but the latter furrow is not joined to the lateral sulcus as it is in *Nycticebus*. The lateral sulcus is a simple arc surrounding the upper ends of the suprasylvian and postsylvian sulci. The latter is bent forward at its upper end, as often happens in *Lemur*. There is a typical well-developed orbital sulcus and also a well-defined coronal.

The most interesting feature of this brain, however, is an extensive transverse furrow, placed between the coronal and lateral sulci in exactly the same manner as the sulcus centralis occurs in its most primitive form in the Apes. This sulcus is obviously formed by a blending of the sulcus *f* of the Lemurs with a sulcus such as I called *x* in *Nycticebus*; in the genus *Lemur* this sulcus is probably represented by the bent piece *c* of the sulcus coronalis. The mesial surface of this hemisphere resembles that of *Nycticebus*.

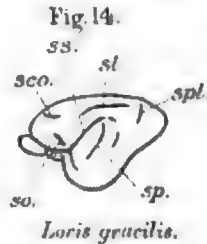
Beddard described a brain of *Perodicticus* (Proc. Zool. Soc. 1895, pp. 144 & 145) which presented features essentially identical with that in the College of Surgeons. His account is marred by the fact that he failed to recognize the lateral [his "angular" sulcus] in *Nycticebus*; and most of his description of the brain of *Perodicticus*, which is concerned with this point, is consequently valueless. He also quite needlessly confuses his account by the misuse of the word "presylvian," which he applies to the sulcus which I have tentatively suggested calling "central." The postsylvian sulcus bends forward as in the last specimen.

Ziehen (Arch. f. Psych. xxviii. p. 901) describes the same brain of *Perodicticus* as myself; but as I had to remove the arachnoid and pia membranes before it was possible to study the arrangement of the sulci, his account can hardly be regarded as an accurate description. His illustration (fig. 3) bears very little resemblance to the specimen in the Royal College of Surgeons, and is obviously adapted from one of Beddard's drawings (*op. cit.* fig. 2 B, p. 145). Ziehen quotes the writings of Beddard, van der Hoeven, and van Camper in reference to the brain in *Perodicticus*.

An examination of the ridges upon the inner walls of the cranium of a specimen of

*Perodicticus* (Royal College of Surgeons, no. 295) reveals a pattern identical with that seen in the actual brain, which I have just described.

In the little brain of *Loris gracilis* the olfactory parts closely resemble those of the other two genera of *Lorisinæ*. The upper ends of the supra- and postsylvian sulci approach very near to one another on the left hemisphere; on the right hemisphere the former is prolonged into a hook surrounding the upper end of the postsylvian. There is a simple arcuate lateral sulcus and a small postlateral. There is a small oblique orbital sulcus; and a shallow furrow placed far forward may represent the coronal sulcus.



Lateral aspect of the left cerebral hemisphere. Nat. size.

There is also a small inferior temporal sulcus on the left hemisphere, as in the brain of *Nycticebus*. On the mesial surface the typical calcarine group and shallow intercalary and collateral sulci are found.

Beddard examined the brain in two specimens of *Loris gracilis*, and stated that "there are only three fissures plainly visible—the Sylvian, the angular [lateral], and the antero-temporal [postsylvian]" (Proc. Zool. Soc. 1895, p. 145). [His representation of the brain (fig. 3) is, however, so studded with innumerable spider-like figures as to be quite unintelligible.] In one of his specimens there was a separate postlateral [his "parieto-occipital"] sulcus on one hemisphere.

Gervais's illustration (Journ. de Zoologie, t. i. pl. 2. fig. 2) is useful as a demonstration of the actual size and shape of the brain in *Loris*; but Beddard's criticism of his representation of the sulci is quite justified. Among the Lemurs it is possible, if the investigator has studied the effect of brain-form on the cranial wall in some members of the Order, to form a very good idea of the configuration of the actual brain from an examination of the brain-case. But Gervais has not exercised sufficient caution in the representation of the plaster casts, and gives an altogether erroneous idea of the configuration of the brain.

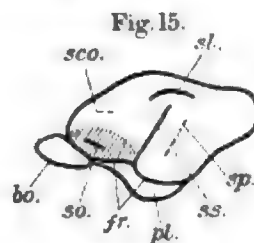
Ziehen's account of the brain in this genus was based upon the specimen in the Royal College of Surgeons and another specimen of his own. He represents the lateral aspect of the left hemisphere (Arch. f. Psychiat. xxviii. fig. 6, p. 908). The Sylvian fissure, orbital sulcus, a very short postsylvian sulcus and a "Scheitelstück" above it, a lateral and postlateral sulcus are all shown; but in addition there is a transverse sulcus labelled  $\epsilon$ , not present in Beddard's specimens nor in that in the College of Surgeons. The letter  $\epsilon$  is used by Ziehen to designate the central sulcus in *Perodicticus*, and both the sulcus which I call  $f$  and that designated  $x$  in *Nycticebus*.

## THE BRAIN IN THE GALAGINÆ.

The brain of *Galago Garnetti* may be regarded as the simplest and most generalized among the Lemurs, if we except that of *Tarsius*, which exhibits a peculiar combination of primitive and pithecoïd features imperfectly disguised by its strangely-distorted form.

The features of the rhinencephalon in *Galago* resemble on the whole those of the Lorisinæ; but the olfactory bulb is plumper and the rhinal fissure is more complete than it is in any other genus among the Primates.

The brain of this species is remarkable (among those of Lemurs of a corresponding size) for the paucity of sulci. Only the most stable and constant sulci are present, and these in a typical and clearly defined form (fig. 15).



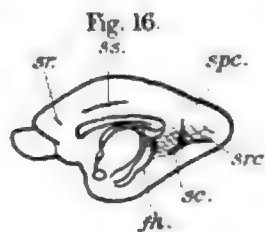
*Galago Garnetti.*

Lateral aspect of the left cerebral hemisphere. Nat. size.

The "Sylvian fissure" is constituted like that of the Lorisinæ, no submerged area being found between its two constituent sulci. The pseudosylvian sulcus is very shallow.

Above the upper end of the suprasylvian (Sylvian) furrow there is a very short lateral sulcus, which is quite straight in one brain, but slightly arched in the other.

There is a simple, straight, clean-cut orbital sulcus parallel to the anterior lateral fissure.



*Galago Garnetti.*

Mesial aspect of the right cerebral hemisphere. Nat. size.

In one of the two brains of *Galago Garnetti* there is a shallow depression far forward on the hemisphere just above the orbital margin: it represents the coronal sulcus.

It resembles the brain of *Lepidolemur* in having no well-defined postsylvian sulcus; but on the left hemisphere of one specimen there is a faint depression in the situation of this furrow. This we have seen to happen sometimes in *Lepidolemur*.



The typical calcarine group of sulci closely resembles that already described in *Nycticebus*. There is a simple linear intercalary sulcus above the anterior two-thirds of the corpus callosum. In one brain there is also a very small oblique rostral sulcus placed far forward on the mesial surface of the hemisphere.

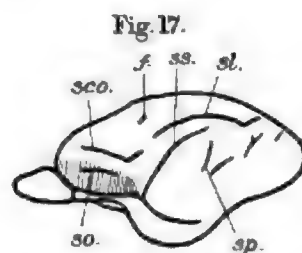
The hippocampal formation presents the typical features, with a large hippocampal tubercle and distinct circumsplenic vestiges.

The cerebral hemisphere is 30.5 mm. long, and its posterior extremity is drawn out into a distinct caudal (or occipital) process. The corpus callosum is 13.5 mm. long, and its splenium is 11 mm. in front of the occipital pole of the hemisphere. The maximum depth of the hemisphere is 19.5 mm.

Although the brain of *Galago crassicaudata* is only a little larger than that of Garnett's species, there is a noteworthy increase in the number and extent of the sulci. This fact becomes more interesting and significant when it is observed that the pattern mapped out by the new sulci is identical with that found in the genus *Lemur*.

The characters of the cerebral hemisphere of the Great Galago may thus be summed up by saying that it is a brain of the same shape as (although slightly larger than) that of Garnett's Galago, with the sulcal pattern of a Lemur.

The upper extremity of the Sylvian fissure bends slightly backward and approaches the upper end of the postsylvian sulcus, as so often happens in the genus *Lemur*. The postsylvian sulcus is represented in the brain in the Royal College of Surgeons merely by a



*Galago crassicaudata.*

Lateral aspect of the left cerebral hemisphere. Nat. size.

short furrow corresponding to its upper end, whereas in Beddard's specimen\* it is the lower end of the sulcus which is deepest. In the skulls of this species which I examined there was a low ridge representing a sulcus as extensive, though not so deep, as that of *Lemur*. The postsylvian sulcus must be regarded as poorly developed in all the Galaginæ. Another instance of this has already been seen in the genus *Lepidolemur*.

In Beddard's specimen the lateral sulcus (which he calls "angular") is represented as a short linear furrow, like that of Garnett's Galago. But in the actual brain (and also in a skull of this species labelled "*Otogale Kirkii*" in the British Museum) I have found evidence of a much more extensive arcuate lateral sulcus surrounding the upper end of the Sylvian fissure. In the brain in the Royal College of Surgeons the posterior end of this sulcus is bent mesially; and at a short distance behind it there are two shallow

\* Proc. Zool. Soc. 1895, p. 146, fig. 4.



transverse furrows (in Beddard's specimen there is only one, which is labelled "parieto-occipital") representing the postlateral (transverse occipital) sulcus. The anterior end of the sulcus extends downward in front of the Sylvian fissure for a short distance, so as almost to reach the caudal end of a sagittal sulcus (coronalis). The latter is bent in an obtuse angle in the brain I have examined; in Beddard's specimen it is apparently represented by two separate sulci (labelled "infero-frontal") in the same straight line; and in the skull of Kirk's *Galago* there is a ridge representing an extensive straight sulcus directed obliquely forward and mesially, as in *Lemur*. Above the sulcus coronalis there is a faint depression (*f*), such as is found in *Lemur*.

On the mesial surface the sulci are grouped as in Garnett's *Galago*. There is, however, a sulcus *a*.

From an examination of the skull of *Galago Monteiri* (Royal College of Surgeons, specimen No. 285, Osteological Series), I can definitely state that the brain is of the same shape as that of Garnett's *Galago*, and presents rhinal and Sylvian fissures and an orbital sulcus of the same type. There must have been, however, an extensive, though shallow, postsylvian sulcus, the upper end of which curves upward and forward toward a lateral sulcus which was prolonged unusually far back. There was also an extensive coronal sulcus, like that of *Lemur*.

In a skull of *Galago Alleni* the most noteworthy feature is the impression of a crescentic or boomerang-shaped coronal sulcus.

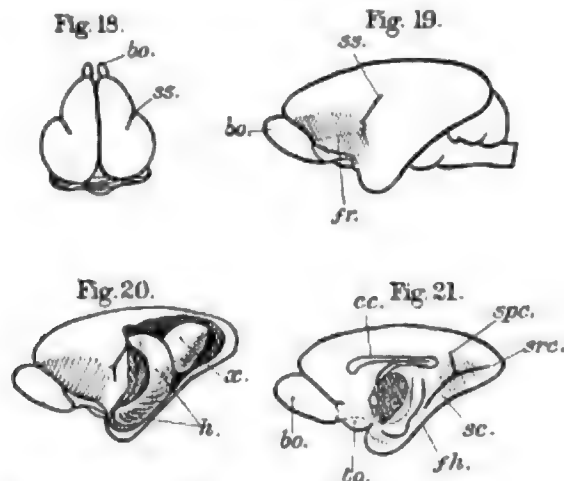


Fig. 18.—*Microcebus Smithi*. Dorsal aspect of the brain. Nat. size.

Fig. 19.—*Microcebus Smithi*. Left lateral aspect of the brain.  $\times 2$ .

Fig. 20.—*Microcebus Smithi*. Lateral aspect of the left cerebral hemisphere, dissected to show the hippocampus and the calcarine eminence.  $\times 2$ .

Fig. 21.—*Microcebus Smithi*. Mesial aspect of the right cerebral hemisphere.  $\times 2$ .

The cerebral hemisphere of the small brain of *Microcebus Smithi* resembles that of *Galago* in shape. It is 15.5 mm. long (without the olfactory bulb, which projects almost 3 mm. in front of the hemisphere); its maximum depth is 10 mm., and its greatest breadth 7.5 mm. (each hemisphere). The lateral caudo-ventral margin is

13.5 mm. long, and is so oblique that its lower end (measured in projection) is 10 mm. further forward than its upper end. The natiform eminence of the pyriform lobe is a very narrow conical projection on the base of the hemisphere. As in the genus *Lemur*, and unlike the condition found in the *Lorisinæ*, the orbital excavation extends back to the Sylvian fissure.

The thin, vertically-placed, leaf-like olfactory bulb resembles that of the *Lorisinæ*.

The rhinal fissure is almost wholly obliterated.

The Sylvian fissure, which is constituted like that of *Galago* and the *Lorisinæ*, extends obliquely upward and backward on to the dorsal surface, and divides the latter into a broadly expanded posterior part (which extends as a thin leaf over the corpora quadrigemina and the anterior part of the cerebellum) and a narrow tapering anterior part.

There is a typically triradiate group of calcarine, retrocalcarine, and paracalcarine sulci, the greater portions of which are situated in the mesencephalic fossa on the lower surface of the caudal region of the hemisphere. There are no other sulci.

The notes on the brain in *Microcebus* and *Chiropate* in the oft-quoted memoirs of Gervais, Beddard, and Ziehen add little more. Beddard records the presence of a very small lateral (his "angular") sulcus (Proc. Zool. Soc. 1895, p. 147).

#### THE BRAIN IN THE INDRISINÆ.

Practically all that is known of the structure of the brain in this subfamily is contained in that part of the 'Histoire Naturelle des Mammifères' of MM. Alph. Milne-Edwards and Alfr. Grandidier which forms volume vi. of Alfr. Grandidier's great 'Histoire de Madagascar.' The other memoirs which refer to the brain of any of the *Indrisinæ*—viz., those of Zuckerkandl and Chudzinski—either add nothing new or are borrowed from Milne-Edwards's great work. Flatau and Jacobsohn derive their account of the brain of *Indris* from Chudzinski, to whom they accord all the credit for a research which is either wholly or for the greater part obviously a reproduction of the account given by Milne-Edwards.

Gervais describes moulds of the cranial cavity in the *Indrisinæ*. He does not seem, however, to have exercised sufficient care in the study of the impressions which correspond to the cerebral sulci. For in the Lemurs, and especially in the genera *Propithecus* and *Indris*, it is possible to accurately map out all the sulci on the outer surface of the cerebral hemisphere, if a critical examination be made of the prominent bony ridges on the inner face of the cranium or of the furrows produced by these ridges on a mould of the cranial cavity.

I have examined a considerable series of crania of the *Indrisinæ* in the British Museum and in the Collection at the Royal College of Surgeons, and have thus been able to gain a much more accurate conception of the plan of the sulci than that conveyed by the lithographs which illustrate the 'Histoire de Madagascar.'

Dr. Forsyth Major lent me an excellent skull of an adult male *Propithecus diadema*,

in which the roof of the cranium had been removed by a clean saw-cut. This I shall adopt as a type.

The cerebral hemispheres were 52 mm. long, 40 mm. broad (*i. e.* 20 mm. each), and approximately 34 mm. deep.

The olfactory bulbs must have been almost, if not quite, completely overlapped by the hemispheres; and about as much of the cerebellum was exposed as is the case in the genus *Lemur*.

The orbital excavation extends back as far as the lower end of the Sylvian fissure; but it does not extend upward to so great an extent as in *Lemur*.

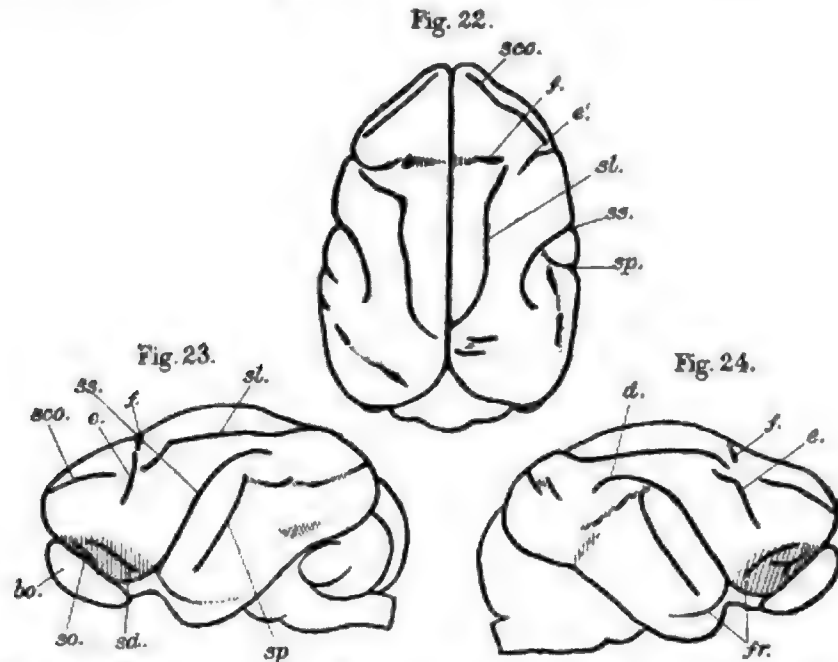


Fig. 22.—*Propithecus diadematus*. Plan of the dorsal surface of the brain. Nat. size.

Fig. 23.—*Propithecus diadematus*. Left lateral aspect of same.

Fig. 24.—*Propithecus diadematus*. Right lateral aspect of same.

The rhinal fissures are much more extensive and complete than they are in any other subfamily of Lemurs (excepting the Galagos), as is well shown in Milne-Edwards's and Grandidier's illustrations ('Histoire de Madagascar,' (2) tome vi. pl. 86. figs. 2 & 3).

The Sylvian fissure does not differ from that of *Lemur*. In this, as in most of the examples of *Propithecus* examined (compare also Milne-Edwards's pl. 86. figs. 1 & 3), the upper extremity of the suprasylvian sulcus is strongly curved backward, being obviously united to the small sulcus (*d*) which is intercalated between the upper ends of the Sylvian and postsylvian sulci in most Lemurs.

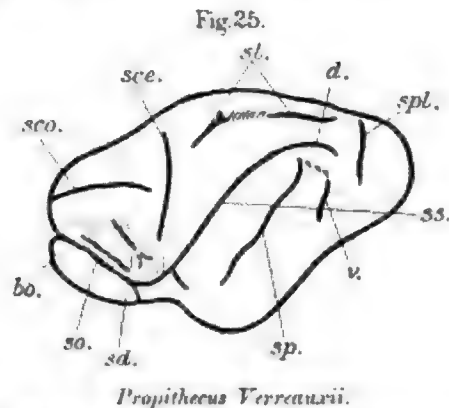
There is a typical postsylvian sulcus, the upper end of which is bent forward (in varying degrees) in all cases. There is a clearly-defined orbital sulcus placed alongside the olfactory bulb. It is subject to great variations in form. On the left hemisphere of this and every other brain which I examined (although Milne-Edwards's case is an exception, *op. cit.* pl. 86. fig. 3) the simple primitive linear form of the sulcus is maintained;

whereas on the right side of this and two other specimens an irregularity is introduced by the development of a side-branch. The diagonal sulcus seems to be more constant in the genus *Propithecus* than in any other Lemur.

In only one case—*Propithecus Coquereli* (fig. 27)—was its presence doubtful; and, as in that particular instance the lateral branch of the orbital sulcus is unusually long and caudally extended, the diagonal sulcus can hardly be regarded as absent even in that case. The other sulci on the outer aspect of the hemisphere exhibit a very interesting and most significant series of variations.

In the type specimen of *Propithecus diadema* (figs. 22, 23, and 24) there are lateral and coronal sulci not unlike those of *Lemur fulvus*, but, in addition, there is a small transverse furrow intercalated between the lateral and coronal sulci, which recalls the ventral extremity of the sulcus termed "central" in *Perodicticus*.

The posterior extremities of the lateral sulci on the two hemispheres curve mesially, as so often happens in the genus *Lemur* when a well-defined postlateral sulcus is not present. There can be little doubt that these mesially-curved extremities of the lateral sulci may be explained in the same way, even though two short transverse furrows are present in the right hemisphere behind the lateral sulci. In a specimen of *Propithecus Verreauxii* (fig. 25), and also in the actual brain of *Propithecus diadema* represented in



Plan of the sulci on the lateral aspect of the left cerebral hemisphere. Nat. size.

the 'Histoire de Madagascar,' (2) tome vi. pl. 86. fig. 1, the presence and position of a definite postlateral sulcus, and the absence of an inwardly-bent tail to the lateral sulcus, clearly complete the demonstration of the identity of these two structures. It is further of interest to note the presence in the actual brain of *Propithecus diadema* of two small transverse furrows such as we have seen in a cast of the same species: seeing that these furrows exist behind a definite separate postlateral sulcus, they afford a further justification for the statements made in the above discussion.

The most instructive features in the brain of *Propithecus* are the varying phases in the group of furrows which we may term "central."

In the only representative of *Propithecus diadema* (figs. 22, 23, and 24) there is a small transverse sulcus in the situation corresponding to that occupied by the little furrow *f* in *Lemur*. On the left hemisphere there is a longer transverse sulcus (*e*)

immediately external to this: it is interposed between the adjacent ends of the lateral and coronal sulci. In Milne-Edwards's specimen of this species the corresponding sulcus is represented as being fused to the coronal sulcus (Hist. Madag. (2) tome vi. pl. 86. fig. 2), just as the coronal sulcus is united to the furrow *e* in *Lemur*, and also in my specimens of *Propithecus Edwardsi* (figs. 28 and 29), *P. Verreauxii* (fig. 26), and *P. Coquereli* (fig. 27). On the right hemisphere of *P. diadema* (figs. 22 and 24) the upper sulcus (*f*) is longer, and the upper end of the lower transverse sulcus (*e*) is bent back behind the end of the lateral.

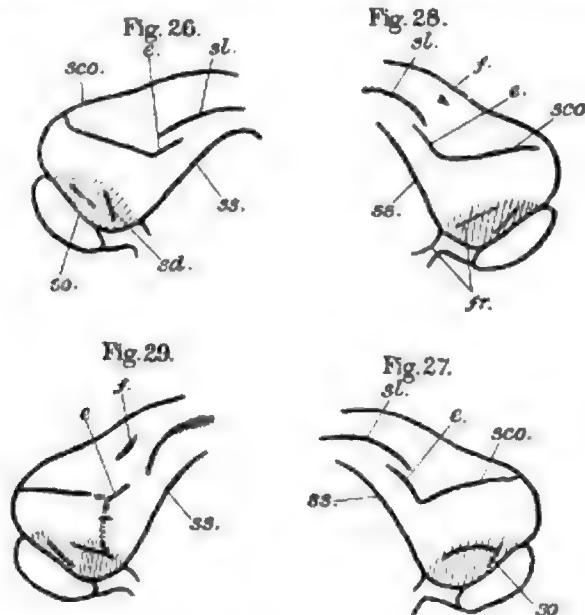


Fig. 26.—*Propithecus Verreauxii*. Plan of the sulci on the anterior portion of another left cerebral hemisphere. Nat. size.

Fig. 27.—*Propithecus Coquereli*. Plan of the sulci on the anterior portion of the right cerebral hemisphere.

Fig. 28.—*Propithecus Edwardsi*. Ditto.

Fig. 29.—Ditto. Left hemisphere.

In the specimen of *Propithecus Edwardsi* (figs. 28 and 29) the arrangement found in *Lemur* is reproduced. The small furrow *f* is oblique, as it is in *Lemur*. On the left hemisphere the upturned caudal appendage (*e*) of the coronal sulcus is apparently separated from the main coronal element.

In *Propithecus Coquereli* there is no furrow *f*, and the sulcus *e* is unusually long (fig. 27). It is joined to the coronal at a right angle, and overlaps the end of the lateral on the caudal side. An exactly similar state of affairs is found in one specimen of *Propithecus Verreauxii* (fig. 26); but in another specimen (fig. 25) of the same species there is a long typical central sulcus, like that found in *Perodicticus*: it clearly represents a fusion of elements *e* and *f* and their complete emancipation from the influence of the coronal and lateral sulci.

The arrangement of the bony ridges corresponding to the cerebral sulci in a cranium

of *Indris brevicaudatus* in the Museum of the Royal College of Surgeons (Osteological Series, No. 253) is represented in fig. 30. The actual brain of a representative of this species has been well represented by Milne-Edwards (Hist. Madag. (2) tome vi. pl. 87. figs. 4, 4a, 4b, and 4c).

The drawings published by Chudzinski (Bull. Soc. Anthropol. vi., vii.), and reproduced by Flatau and Jacobsolin (Handbuch, p. 203), appear to be borrowed from the figures 4 and 4b of Milne-Edwards's work.

In my specimen (fig. 30) the upper end of the suprasylvian sulcus is strongly recurved, as it is in *Propithecus*. There is an unusually long postlateral sulcus, as there is also in Milne-Edwards's specimen. In the skull the ridge for the lateral sulcus was shallow and ill-defined, and seemed to be broken into three parts ( $l'$ ,  $l''$ , and  $l'''$ ), of which only the anterior ( $l'''$ ) was prominent. It seemed to be joined to the coronal

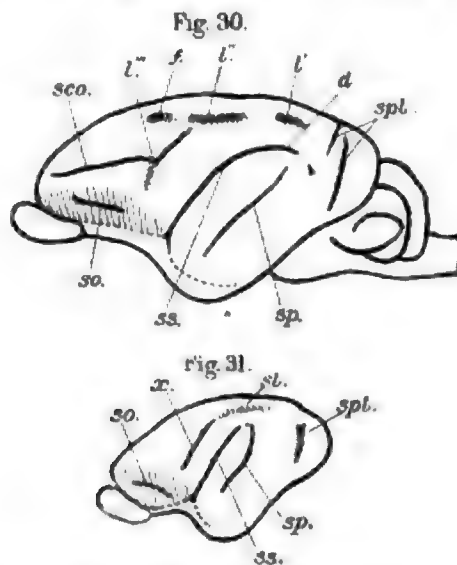


Fig. 30.—*Indris brevicaudatus*. Left lateral aspect of a cranial cast. Nat. size.

Fig. 31.—*Avahis laniger*. Lateral aspect of the left cerebral hemisphere. Nat. size.

sulcus, which was much longer than in Milne-Edwards's specimen. Judging from the condition represented by Milne-Edwards in the actual brain, I am inclined to regard all three furrows,  $l'$ ,  $l''$ , and  $l'''$ , in my specimen as representing the lateral sulcus. But the relationship of the sulcus  $l'''$  to the coronal seems to indicate that the former sulcus may also represent the furrow  $e$  of *Propithecus* (compare figs. 26, 27, 28, and 29), which may have fused with the lateral sulcus. This is a matter which can only be settled by a careful study of a series of actual brains. This suggestion is put forward merely as the solution which seems most likely to be correct.

Chudzinski regards the sulcus which is formed by the union of the furrows  $l''$  and  $l'''$  in Milne-Edwards's specimen as the "central sulcus." But there is in both specimens a small sagittal sulcus  $f$ , which represents the similarly-labelled furrow in *Propithecus* and *Lemur*.

The orbital sulcus is large and asymmetrical in the two hemispheres.

The mesial surface of the hemisphere in the Indrisinæ is known to me only in the drawings (Hist. Madag. (2) tome vi. pl. 86. fig. 6, pl. 87. figs. 2*b* and 4*c*) of Milne-Edwards's monograph. It closely resembles that of *Chiromys*, which will be described later on in these notes.

Nothing is known of the smaller brain of *Arahis* except the scanty information contained in Milne-Edwards's memoir. The plan of the ridges on the interior of a cranium of *Arahis laniger* (in the Royal College of Surgeons) is shown in fig. 31.

There are well-defined representatives of the Sylvian, postsylvian, and orbital sulci, shallow lateral and postlateral furrows, and also a deep sulcus *x* (in apparent continuity with the lateral sulcus) running parallel to the Sylvian fissure. Comparison with the brain of *Indris* (fig. 30) seems to point to an homology with the element *l''* in that genus. Comparison with the plan found in *Propithecus* (compare fig. 24) seems to suggest its identity with the sulcus *f* of that genus. In Milne-Edwards's specimen it is not so distinctly transverse in direction. In my specimen there is no trace of any ridge corresponding to the coronal sulcus. All this variability of the furrows around the adjacent ends of the lateral and coronal sulci in the Indrisinæ shows how unstable this region is in these animals. This instability is probably due to two distinct factors. In the first place, this area is the seat of very pronounced growth-changes in all the Primates, and especially the lowlier members of the Order, because the excitable area of the cortex is expanding to a much greater extent than in other mammals. At the same time, there is in the Lemurs, and especially the Indrisinæ, another and a greater disturbing factor, which is the pronounced tendency to a disintegration of composite sulci: this must be the expression of some retrogressive process of evolution. This variability is perhaps best exemplified by the behaviour of the sulcus *f*, which seems to be linked in different individuals of the Indrisinæ to the coronal sulcus, the sulcus *c*, and even to the lateral sulcus.

#### THE CEREBRAL HEMISPHERES IN THE GENUS DAUBENTONIA (more commonly called *Chiromys*).

The brain of the Aye-aye (*Daubentonia madagascariensis*, Geoff., *Chiromys madagascariensis*, Cuv.) is of extraordinary interest to the morphologist by reason of the possession of what Chudzinski calls "contradictory characters." The same writer further explains this remark by the statement that although the Aye-aye is no larger than a small rabbit, or even not so big, it has a most voluminous brain, very rich in cerebral folds\*. He adds that "the form of the brain is ovoid, but its anterior extremity is markedly rounded. In this respect it resembles the brain of certain Rodentia (*Castor*, *Hystrix*) and even certain Marsupials (*Phascolomys*). Although these comparisons are quite justified, resemblances of a closer character are to be found within the Prosimiæ themselves. Gervais describes the cranial cast of the Aye-aye as being "plus arrondi et plus bombé à sa face supérieure que celui des Makis, du Propitèque et de l'Indri" †. He compares the appearance of its upper surface with that of the Carnivore *Ailurus fulgens*.

\* Bull. Soc. Anthropol. sér. 4, vii. 1896, p. 13.

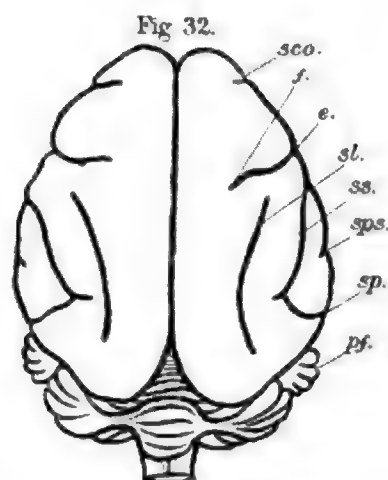
† Journ de Zool. i. 1872, p. 23.



The olfactory bulb is a flattened cake-like mass 9 mm. wide and 11 mm. long, and resembles that found in the Indrisinæ and in the genus *Lemur*. It is, however, completely overlapped by the cerebral hemisphere, as Oudemans and Chudzinski have already pointed out; Gervais's representation of it projecting beyond the hemisphere like that of *Lemur* is clearly erroneous.

About as much of the cerebellum is uncovered by the cerebrum as we have noted in one specimen of *Lemur fulvus* (fig. 3).

The arrangement of the cerebral sulci presents some most extraordinary features: it is, moreover, especially noteworthy by reason of its extreme variability. The plan of the furrows is so puzzling that no writer on the brain of *Chiromys* has ventured to compare it in detail with that presented by other Lemurs. Thus, Owen makes use of the nomenclature used in describing the brain in the Carnivora; Gervais compares it with



*Chiromys madagascariensis.*

The dorsal aspect of the brain. Slightly enlarged.

that of *Ailurus*; Oudemans likewise employs Krueg's nomenclature for the Carnivore-brain; Chudzinski also is driven to a comparison with the cerebral pattern in the same Order; and, finally, A. J. Parker\* quotes with approval the opinion of Pansch that the Aye-aye belongs to the group of mammals which includes the Carnivora.

The chief reason for all this hesitancy in comparing the sulci of this brain with those of the other Primates depends upon the fact that in *Chiromys* the suprasylvian sulcus has become widely separated from the pseudosylvian sulcus, and the latter is exhibited in different specimens in various stages of disintegration. Thus there is no typical Sylvian fissure; and the failure to recognize that the latter consists (in the other Primates) of an *apparent* blending of the suprasylvian and pseudosylvian sulci by the submergence of the region between the overlapping parts of these furrows (*vide supra*) naturally gives rise to confusion when the intervening area is *not* submerged, as is the case in *Chiromys*. This separation of suprasylvian and pseudosylvian sulci also makes

\* Journ. Acad. Philad. ser. 2, x. 1896.

the resemblance of the pattern to that found in the Carnivora much more obvious than it is in other Lemurs, and, to a certain extent, justifies the comparison which all previous writers have instituted.

It was, in fact, the search for an explanation for the extraordinarily puzzling arrangement of the sulci in the brain of *Chiromys*, which led me to conclude that the suprasylvian sulcus becomes merged in the "Sylvian fissure" in the Primates—an hypothesis the accuracy of which has been so amply confirmed by later studies.

In one brain, which I shall distinguish as  $\alpha$ , a deep furrow begins near the bend of the rhinal fissure, and passes upward with a very slight backward inclination for a distance of about 11 mm. This is the pseudosylvian sulcus (figs. 33 and 34).

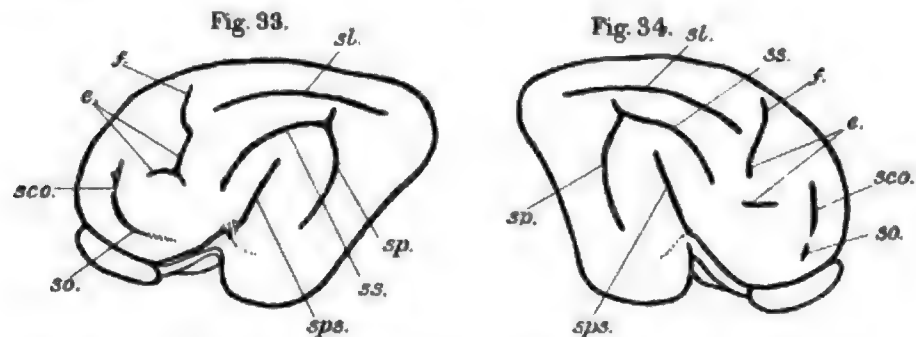


Fig. 33.—*Chiromys madagascariensis*. Lateral aspect of the left cerebral hemisphere.

Fig. 34.—Lateral aspect of the right cerebral hemisphere.

An arched furrow formed by the union of the suprasylvian and postsylvian sulci, after the manner of the pattern found in the Carnivora, surrounds the pseudosylvian sulcus (figs. 32, 33, and 34). The suprasylvian sulcus begins at a distance of 5 mm. in front of the upper part of the pseudosylvian, and arches obliquely upward and backward to a point 15.5 mm. from the mesial plane and 12.5 mm. in front of the posterior margin of the hemisphere. At this point it joins the postsylvian sulcus, and from the conjoint furrow a little upwardly-directed branch 2 mm. long is given off. The postsylvian sulcus is 8.5 mm. behind the pseudosylvian sulcus. The two hemispheres of the specimen  $\alpha$  are practically symmetrical so far as these features are concerned.

In a second specimen (figs. 35 and 36), which I shall distinguish as  $\beta$ , the suprasylvian sulcus presents similar features to those just described in  $\alpha$ ; but the postsylvian and pseudosylvian have become so greatly distorted and broken up that a pattern is formed which is quite unlike that exhibited by the specimen  $\alpha$ .

On the left hemisphere there is a much shorter and shallower pseudosylvian sulcus. The suprasylvian sulcus is separated from a very oblique sulcus (which is analogous to the upper part of the postsylvian) by a narrow gyrus (fig. 35). And between this and the small pseudosylvian there is a vertical sulcus ( $x$ ) which is much longer and deeper than either of the furrows between which it lies. It is clearly a furrow compensatory to the fragmentary pseudosylvian and postsylvian sulci. Behind it there is a much

shorter furrow (*y*), placed below the displaced upper postsylvian element (*w*). This represents another fragment of the postsylvian sulcus.

In the right hemisphere the pseudosylvian sulcus is represented by a very shallow depression, which is not worthy to be called a sulcus except in the uppermost 2 millimetres of its extent. The oblique sulcus *w* is here joined to the suprasylvian. The sulci *x* and *y* are practically symmetrical on the two hemispheres. It seems probable that the little ascending branch of the arcuate sulcus in the specimen *α* belongs to the postsylvian sulcus. In a series of crania of *Chiromys* which I have examined, the condition of the suprasylvian, pseudosylvian, and postsylvian sulci most nearly resembles that seen in the specimen *α* in all cases.

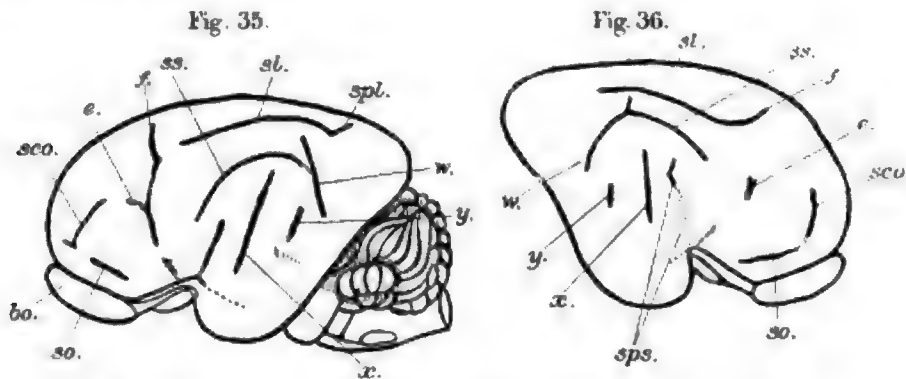


Fig. 35.—*Chiromys madagascariensis*. Left lateral aspect of another brain.

Fig. 36.—*Chiromys madagascariensis*. Lateral aspect of the right hemisphere.

In the two crania numbered 302 and 302 B in the Collection of the Royal College of Surgeons, the bony ridge corresponding to the suprasylvian sulcus is much nearer to the well-defined ridge representing the pseudosylvian sulcus (in all four hemispheres) than the corresponding sulci are in the brain *α*. In the skull numbered 302 the postsylvian ridge seems not to be joined to the suprasylvian. But in the other cranium, as well as in one of those in the British Museum, the suprasylvian and postsylvian ridges unite to form a regular arc.

In Oudemans's specimen the arrangement of the sulci appears to have been even more distorted than it is in my specimen *β*. Thus on the left hemisphere (*op. cit.* pl. iii. fig. 11) the suprasylvian sulcus (which he labels "Sylvian") is widely removed from the small upper fragment of the postsylvian (which he correctly labels "suprasylvia posterior"). There is no sulcus corresponding to that which I labelled *y* (fig. 35), but there is a well-defined sulcus *x*, which Oudemans regards as part of the postsylvian (his "suprasyl. post."). There are also two furrows radiating from the angle of the rhinal fissure—one (which he does not label) passing to the representative of the sulcus *x*, and the other (which he calls "Sylvian") passing vertically upward *in front of* the lower end of the suprasylvian. On the right hemisphere (*op. cit.* pl. iii. fig. 12) these two sulci (suprasylvian and the last described) are united: the two sulci which appear to represent (this is merely a rough comparison, for no exact homology can exist) the furrows *w* and *x* in my specimen *β* are united to form a very sinuous sulcus.

Oudemans explains this exceedingly puzzling condition in these words:—"Die Fissura Sylvii zeigte sich an der rechten Hemisphäre viel mehr ausgeprägt als an der linken. Nur der obere Theil derselben war tief einschneidend, der untere mehr superficiell, besonders an der linken Hemisphäre, wo beide Theile selbst getrennt waren. Das wir es hier jedoch gewiss mit der Fissura Sylvii zu thun haben, ergab sich durch Vergleichung mit den Gehirnen einiger anderen Lemuriden." (Naturh. Verh. Akad. Amst. xxviii. p. 28.)

The closing phrase is true, but the writer misses the obvious inference, which must follow from this important fact, viz.—that the Sylvian fissure of the Lemurs is partly represented by the suprasylvian sulcus. In order to evade this conclusion, in deference to the popular belief in the identity of the so-called "Sylvian fissure" of Carnivora and the Prosimian Sylvian fissure, Oudemans is forced to call the lateral sulcus "suprasylvian." [For if the real suprasylvian is considered as representing the "feline Sylvian," it is not illogical to call the lateral sulcus by the name "suprasylvian," even if such an hypothesis makes it necessary to suppose that the lateral sulcus has disappeared.] It was unfortunate for Oudemans that he did not chance to see such a specimen as my example  $\alpha$ ; for then there could have been no doubt that the Lemuroid Sylvian fissure is also in great part identical with the suprasylvian sulcus.

Chudzinski, who happened to have a specimen which (so far as I am able to judge from his unsatisfactory account) resembled my specimen  $\alpha$ , failed to recognize the suprasylvian sulcus as the Lemuroid "Sylvian."

He regards the pseudosylvian sulcus as the Sylvian fissure, and says that it is joined to the rhinal fissure (which he calls the fissure of the olfactory lobes) on the right side but not on the left (Bull. Soc. Anthropol. sér. 4, vii. pp. 13 & 14). [This difference between the two hemispheres also seems to occur in my specimen  $\alpha$ , but the condition of the brain prevents me from speaking more decisively.] He is then so puzzled by the suprasylvian and postsylvian sulci, that he does not attempt to compare them with the sulci of the Primates, but, like all previous writers, seeks an analogy to the condition found in the Carnivores (*op. cit.* p. 16). His specimen seems to have been exceptionally interesting, and it is therefore very disappointing to find such imperfect drawings and such vague descriptions, from which it is impossible to form a clear conception of the condition. The postsylvian sulcus seems, if I read the account correctly, to be independent of the suprasylvian on the right side; and the latter appears to be so related to the pseudosylvian as to be very slightly if at all different from the normal Prosimian Sylvian fissure [but this is by no means clear].

One cannot fail to be amazed that Chudzinski, who during the previous year had been studying the brain in *Lemur*, *Nycticebus*, and *Indris*, should have failed to recognize in the suprasylvian sulcus of *Chiromys* the homologue of the upper part of the Sylvian fissure of these Lemurs.

It is difficult to form a clear conception of the condition of Owen's specimen from his imperfect lithographs and vague description; and the interpretations of it by succeeding writers (such as Pansch, Beddard, and Parker) only tend to still further confuse the issues.

The remarks of Gervais are of interest only in so far as they call attention to the presence of an additional arcuate sulcus [*i. e.* the separation of the suprasylvian and the pseudosylvian sulci] without suggesting any solution.

In my specimen  $\alpha$  the lateral sulcus begins posteriorly at a point 8 mm. from the mesial plane and an equal distance from the posterior margin; the anterior extremity is 11.5 mm. from the mesial plane and 16 mm. from the anterior extremity of the hemisphere. The sulcus is 23 mm. long. In none of my specimens, nor in that of Oudemans, can I find any trace of a separate postlateral sulcus, but in the left hemisphere of the specimen  $\beta$  there is a characteristic mesially-bent tailpiece such as we have seen representing the postlateral sulcus in many Lemurs.

The furrows which are situated in that region of the hemisphere which lies in front of the lateral and suprasylvian sulci are subject to considerable variation. On the left hemisphere of the specimen  $\beta$  there is a typical orbital sulcus, and in a more dorsal position a very obliquely placed sulcus, which a comparison with other Prosimian brains clearly shows to be the anterior part of the coronal sulcus. On the right hemisphere of the same brain a shallow depression unites these two furrows. On the left hemisphere of specimen  $\alpha$  they are joined to form a single transversely-placed arcuate furrow; on the right hemisphere the orbital furrow has disappeared and there is simply a transverse coronal element. In two of the crania (302 and 302 B) to which I have referred, the two sulci are well developed and united to form figures, one like a crescent, the other like a letter U placed on its side.

These sulci are exhibited in a typical manner in Oudemans's memoir, and the names "presylvian" and "proreau" which he applies to them we shall find in the subsequent discussion to be not inappropriate.

Midway between the sulcus which I have called coronal and the anterior ends of the lateral and suprasylvian sulci respectively, there are two sulci in the left hemisphere of the specimen  $\beta$ . The upper of these may be compared with the sulcus distinguished by the letter *f* in *Lemur*, and the lower one with that called *e*. These two sulci are united by a shallow furrow to form a long transverse "sulcus centralis" (fig. 35).

On the right hemisphere of the same brain (fig. 36) the two furrows *e* and *f* are much smaller and are widely separated. The sulcus *f* is joined to the anterior end of the lateral sulcus, and *e* remains as a short independent furrow widely separated from all the other sulci on the hemisphere.

On the left hemisphere of the specimen  $\alpha$  (fig. 33) the two sulci *e* and *f* are united at an obtuse angle, and the former has a horizontal ramus, which recalls the fact that it is really the posterior fragment of the coronal sulcus. On the right hemisphere of this brain the horizontal sulcus is independent of the moderately long central one.

On the right hemisphere of Oudemans's specimen there is a small triradiate sulcus *f* (which he calls "coronal"), and a horizontal sulcus exactly like that exhibited by the right hemisphere of my specimen  $\alpha$ . This he calls "prorean," *i. e.* the same name by which he denotes the anterior element which I call "coronal." This is of interest in so far as he gives the same name ("prorean") to these two widely-separated furrows, which I also regard as two fragments of one sulcus ("coronal"). On the left hemisphere of

his specimen the *f* element is a larger transverse sulcus and the *e* element is a small Y-shaped furrow, which might possibly be explained by the condition seen in the left hemisphere of my specimen *a*.

On both sides of three crania which I examined there is a long ridge representing a fairly extensive "central sulcus," such as might be produced by a deepening of the connection between the furrows *e* and *f* on the left side of my specimen *β*.

If we summarize all this puzzling variety in the arrangement of the furrows on the outer surface of the hemisphere of *Chiromys*, the great outstanding fact is revealed that, amidst all the variations which so modify as almost to disguise the identity of most of the sulci, the suprasylvian and lateral sulci alone remain unchanged. They are the deepest and most stable sulci on the outer surface of the hemisphere.

The other feature of interest is the strongly marked tendency toward the formation of a transverse sulcus from the elements *e* and *f*, which is either the homologue of the central sulcus or, at least, in the present state of our knowledge, fulfils all the known criteria of a sulcus of Rolando.

The peculiar variations which have been noted in the cerebral hemisphere of *Chiromys* can only be explained on the supposition that a large and highly convoluted brain is undergoing a process of retrograde metamorphosis which leads to the disintegration of all except the most stable sulci. It is altogether inconceivable that the unstable group of fragmentary sulci which represent the pseudosylvian, postsylvian, and coronal sulci can be stages in the evolution of a more complex pattern of furrows. All these facts point to the conclusion that *Chiromys* is not the lowly Carnivore-like primitive Lemur which most other writers on cerebral anatomy suppose, but a highly-specialized Primate which has undergone most pronounced retrogressive changes, as the result of which all the more variable features of its brain stand revealed and, by contrast, show the underlying common mammalian features, which are the heritage of all the Meta- and Eutheria.

None of the writers who have described the brain of *Chiromys* has placed on record any information concerning the mesial surface of the hemisphere. I have examined this aspect in four examples.

The corpus callosum is 23 mm. long and very plump, with a considerably thickened splenium. Its anterior part is bent downward so as to be boomerang-shaped (fig. 37). This is unlike that of the other Lemurs, and may possibly be due to a retraction of the anterior regions of the hemisphere, when the latter lost the more pointed form which it must have had in the immediate ancestors of *Chiromys*. For the peculiar blunt anterior pole of the hemisphere cannot be primitive, and when this process took place it probably influenced the form of the corpus callosum on the mesial surface, just as it has modified the coronal sulcus on the lateral aspect of the hemisphere.

The hippocampus is distinguished by the possession of an unusually large hippocampal tubercle (fig. 38), and also possesses that peculiar furrow (*a*) which we have seen in the genus *Lemur*. I know of no brain other than those of the Primates in which these two peculiarities are both found. The particular form they assume in *Chiromys* is distinctly Prosimian.

The most interesting feature on the mesial surface is the grouping of the sulci.



The first cerebral hemisphere of the Aye-aye, which I examined, is that represented in fig. 38. At that time I had just completed an investigation into the morphology of the calcarine sulcus, and had come to the conclusion that the homologue of the [anterior] calcarine sulcus of the Primates was to be found in the retrosplenial part of the splenial sulcus of Krueg in the brains of Carnivora, Ungulata, Edentata, Chiroptera, and Marsupialia (Proc. Anatomical Soc. of Gt. Britain and Ireland; Journ. Anat. and Phys., 1899). In this particular hemisphere of *Chiromys* there seemed, at a casual glance, to be one great arcuate sulcus (such as we find in *Tapirus*, for example) representing a fusion of the genual, intercalary, and calcarine sulci; and so, occurring in a Lemur,

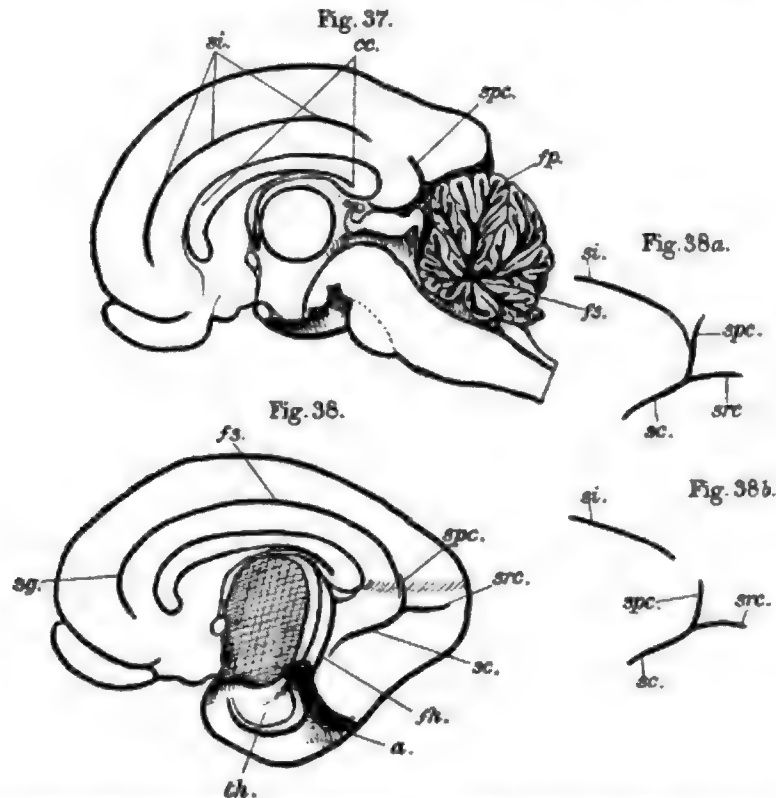


Fig. 37.—*Chiromys madagascariensis*. Mesial aspect of the brain cut in sagittal section.

Fig. 38.—*Chiromys madagascariensis*. The mesial aspect of the right cerebral hemisphere.

Figs. 38 a, b.—*Chiromys*. Modifications of the calcarine group of sulci, delineating the variations as if they occurred in the right hemisphere, so as to be more directly comparable with figs. 37 and 38.

there seemed to be a striking confirmation of the hypothesis I then put forward. However, upon separating the lips of the sulcus in the region immediately behind the splenium, the great arcuate sulcus was found to be interrupted by a small narrow submerged gyrus, so that the essential relations of the two furrows were those diagrammatically shown in fig. 38. Examination of the other hemisphere showed the existence of a broader bridge, and thus exposed a state of affairs which is essentially identical (fig. 38 b) with that found in other Lemurs. The subsequent examination of a second brain still further confirmed this view. In these four hemispheres of *Chiromys* we find therefore every gradation of form between a condition which differs in the very



slightest degree from that common mammalian form, such as the brain of *Tapirus* exhibits, to the characteristic Prosimian or Primate condition. The persistence of the narrow gyrus between the intercalary and paracalcarine sulci, when the mechanical conditions clearly predispose to the fusion customary in non-Primates, is yet another testimony to the view that *Chiromys* is a retrograde Primate.

The calcarine sulcus begins at a point 8 mm. below the splenium of the corpus callosum and 2 mm. behind the hippocampal fissure; it proceeds obliquely upward and backward to a point 5 mm. behind and slightly below the level of the splenium: there it bifurcates into retrocalcarine and paracalcarine branches. The former proceeds horizontally backward and the latter vertically upward. In one instance the paracalcarine is separated from the rest of the great cingular sulcus by a narrow submerged strip (fig. 38): in another case (fig. 38a) there is also merely a very narrow strip separating the sulci, but the upper end of the paracalcarine is prolonged beyond the region of approximation. This is the condition which Milne-Edwards (and Chudzinski after him) represents as being the usual form in the Indrisinæ.

#### THE BRAIN OF THE EXTINCT LEMUROID GLOBILEMUR.

In 1897 Dr. Forsyth Major described \* a plaster mould of the cranial cavity of the large sub-fossil Lemuroid to which he had previously given the name *Globilemur Flacourti*.

I would not have deemed it necessary to attempt to add anything to the clear and sufficient (*i. e.* considering the state of the material) account given by this excellent anatomist, if his memoir had not been recently criticised by Rudolf Burckhardt. Whilst I was actually engaged in studying the plaster mould and the cranium from which it was made in the British Museum, my attention was called to the brief report of Burckhardt's criticism, which was then just published †. I therefore carefully re-examined in the light of these criticisms the crania and the casts of *Globilemur* [and also of *Megaladapis*, to which I shall refer later in this memoir]. Professor Burckhardt has just been good enough to send me a copy of the full memoir ‡, of which the above-quoted note may be regarded as an abstract.

The brain of *Globilemur* was considerably larger than that of any living Lemur. It had large flattened olfactory bulbs projecting very slightly beyond the apex of the hemisphere, as in the genus *Lemur*. In fact the whole of the exposed part of the rhinencephalon closely resembles that of *Lemur*.

The cerebral hemispheres (fig. 39) cover the cerebellum to a slightly greater extent than in most members of the genus *Lemur*; the obliquity of the postero-inferior margin of the hemisphere is about the same as in *Lemur* (fig. 40). In respect to both of these points, Burckhardt's drawings are misleading (*op. cit.* fig. 1, p. 231).

So far as the shape of the hemispheres is concerned, this cast differs from that of any of the larger Lemurs, such as *Chiromys*, *Indris*, *Propithecus*, and *Lemur*. It is least

\* Proc. Royal Soc. 1897, pp. 46 & 47, pl. 5, figs. 1, 2, and 3.

† "Tageblatt des V. Internationalen Zoologen-Congresses," Berlin, August 1901, Nummer 4, 14th August.

‡ "Das Gehirn zweier subfossiler Riesenlemuren aus Madagascar," Anatomischer Anzeiger, Bd. xx. 1901, pp. 229-232, fig. 1, a & b.

unlike the latter, but the extreme broadening of the hemisphere posteriorly and the more pronounced tapering of its anterior part give the brain (as a whole) an oval form, which is quite unlike that of *Lemur*. Forsyth Major compares its shape to that of *Microcebus*; on the whole I think that the dorsal contour of the brain approaches nearest to that of the smaller Cercopithecidæ.

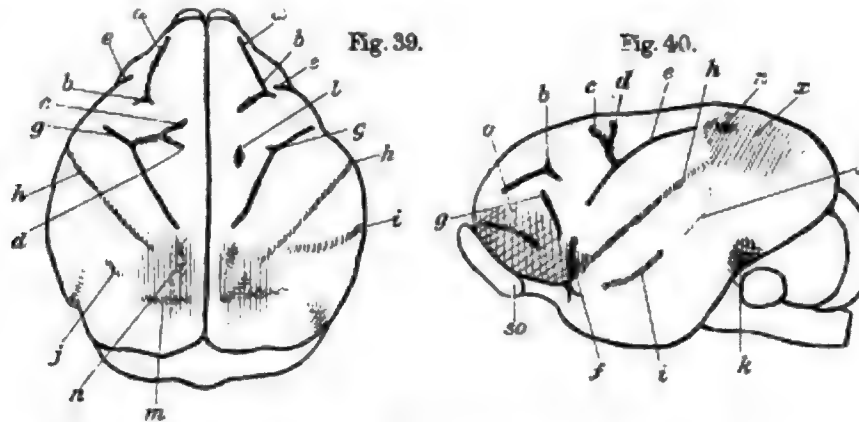


Fig. 39.—*Globilemur Flacourti*. The dorsal aspect of a cranial cast.  $\times \frac{1}{2}$ .

Fig. 40.—*Globilemur Flacourti*. The left lateral aspect of the same.  $\times \frac{1}{2}$ .

The problem of mapping-out the pattern of the cerebral sulci in this brain is one of singular and unexpected difficulty. In most Lemurs and in many of the Cebidæ the positions and extent of the various sulci can be determined with the greatest ease and certainty. But in the crania of most Apes the ridges which correspond to the position of the cerebral furrows become blurred and indistinct in the greater part of the surface, excepting only the anterior region, which contains sharply-defined elevations representing the sulci rectus, arcuatus, orbitalis, and fronto-orbitalis.

If a series of crania of Cercopithecidæ be examined, it will be found in many of them that all the ridges behind that representing the sulcus arcuatus are so indistinct that it would not be easy to map out the sulci, if we did not happen to know the plan. It is a peculiar fact that the ridge for the Sylvian fissure, which is always so distinct in the Lemurs, becomes almost completely obliterated in the crania of many Apes. And the crests representing the intraparietal, the parallel, and, in a less marked degree, the central sulci share a like fate.

A similar state of affairs is unfortunately present in *Globilemur*; so that it is quite impossible to map out the position of most of the sulci. As in the Apes, the ridges representing the sulci on the anterior region of the hemisphere are by far the most distinct.

Thus there can be no doubt concerning the recognition of the orbital (*a*) and coronal (*b*) sulci (figs. 39 & 40). There is a prominent bony ridge representing a furrow skirting the fronto-orbital margin of the hemisphere, which is probably the diagonal sulcus (*e*). But the determination of the identity of the other furrows offers insuperable difficulties.

In both hemispheres there is a short vertical furrow (*f*), which both Forsyth Major and Burckhardt consider to be the representative of the Sylvian fissure or part of it.

The latter writer regards the furrow *g* to be the upper part of the Sylvian fissure, which is separated from the lower part (*f*) by "eine kleine Unterbrechung, die jedoch nur auf Rechnung des Schädelaugusses zu setzen ist" (Anat. Anz. 1902, p. 231). Natural though such a suggestion is at a casual glance, its adoption would logically lead to many difficulties in the interpretation of other furrows. Thus it is quite inconceivable that the lateral (intraparietal or "interparietal" of German writers) sulcus, which we have learnt to regard as one of the most stable sulci, not only in the Lemurs but also in the other Mammalia, can be represented merely by the furrows *d* and *n*. The former of these (*d*) is not even present on the right hemisphere, and *n* is so shallow as to be of questionable value. Moreover, if *n* is part of any furrow, it is that marked *g*, and not *d*, to which it must be linked. If Burckhardt had suggested that the lateral (intraparietal) and the suprasylvian (Sylvian) sulci had fused as in *Nycticebus*, *Chrysothrix*, and *Nyctipithecus*, there would have been less reason for criticising his suggestion on this particular point. But there are other reasons which forbid us accepting the suggested homology as the true interpretation. It is hardly probable\* that a hemisphere which has extended backward over the cerebellum to an extent at least as great as ever occurs in *Lemur* should possess a Sylvian fissure which slopes backward so much more slightly and occupies such a forward position. And if *g* is the Sylvian fissure and *h* the superior temporal, as Burckhardt suggests, it necessarily follows that half of the cerebral hemisphere lies on the caudal side of the latter sulcus! This would be a state of affairs for which no parallel exists elsewhere in the Primates.

I do not think that Burckhardt's suggestions are at all conclusive or even probable. But, on the other hand, I cannot offer any alternative scheme which is not open to adverse criticism. If the furrow *f* had not been present† I should have confidently believed that this brain retained the true Lemurid pattern of sulci, *g* + *n* being the lateral, *h* the Sylvian, and *i* + *j* being the postsylvian; but now I cannot do more than subscribe to the opinion of Forsyth Major that "it is never safe to attempt to make out the exact homologies of the fissures in a cast of the brain-cavity" (*op. cit.* p. 47).

#### THE BRAIN IN MEGALADAPIS.

One can speak with much more confidence concerning the features of the brain in *Megaladapis madagascariensis*, Maj.; but most that deserves saying concerning this brain has already been admirably said by Dr. Forsyth Major‡.

The great contrast which the shape of this brain presents to that of *Globilemur* and the extraordinary conformation of its anterior parts (more especially the elongation of the olfactory peduncles and the relatively forward position of the optic chiasma) have been clearly shown in the figures and descriptions of the work just quoted. The

\* In making this statement I have not forgotten that the Sylvian fissure may occupy such an unusual position, as, for instance, in *Tarsius*.

† In the skull of a specimen of *Nycticebus* I have seen a bony ridge in a corresponding situation, which did not represent any furrow on the brain itself.

‡ Proc. Roy. Soc. 1897, pp. 47-50.

essential features are represented diagrammatically in the accompanying sketches (figs. 41 & 42).

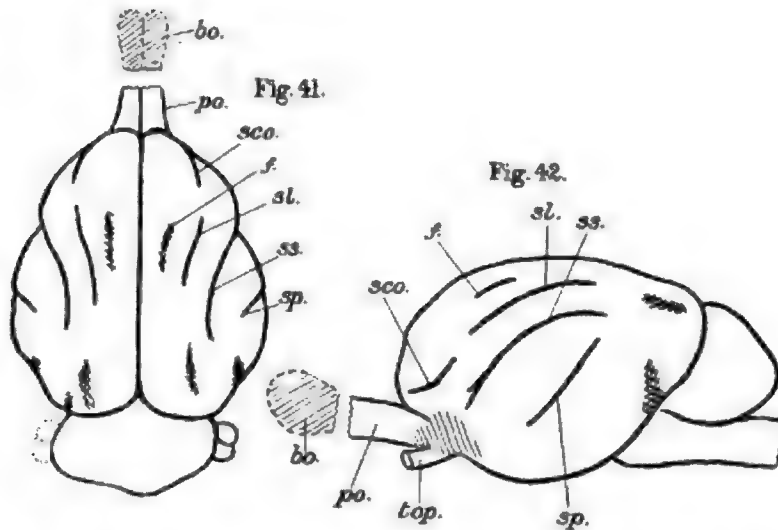


Fig. 41.—*Megaladapis madagascariensis*. The dorsal aspect of a cranial cast.  $\times \frac{1}{2}$ .

Fig. 42.—*Megaladapis madagascariensis*. The lateral aspect of the same.  $\times \frac{1}{2}$ .

The form of the brain (especially the full rounded blunt anterior ends of the hemispheres and the absence of a fronto-orbital edge) resembles that of *Chiromys*. The arrangement of the furrows approximates most nearly to that seen in the Indrisinae and especially *Indris*. They are, however, fewer in number and simpler than they are in the latter. There can be little doubt as to the identity of the suprasylvian, lateral, coronal, and postsylvian sulci, and the furrow *f* represents the similarly-labelled sulcus in other Lemurs. The apparent absence of the orbital sulcus is noteworthy. Burekhardt's extraordinary suggestion that the furrow which I have called "lateral" represents the precentral sulcus is peculiar, because no central sulcus is present; but it is preposterous to represent as the precentral a furrow which, according to his diagram (*op. cit.* p. 233, fig. 2 A), is placed parallel to and on a lower plane than the frontal sulcus.

But the most unwarrantable statements in Burekhardt's work are those accusing Forsyth Major of mistaking the optic nerves for the olfactory bulbs. The latter anatomist had carefully studied and described the skull of *Megaladapis*\* long before he attempted to describe the plaster mould of its cranial cavity. He was therefore labouring under no misconception as to which lacunæ in the cranial wall were the optic foramina and which depressions were the olfactory fossæ. So that when he came to describe the cranial cast, there was no difficulty in recognizing as such the optic nerves (even though their position is so peculiar) and the olfactory peduncles (greatly elongated though they are). In the account which Burekhardt criticises, the conformation of the cranial region surrounding the disputed brain-area is carefully described (*Proc.*

\* "On *Megaladapis madagascariensis*, an extinct gigantic Lemuroid," *Phil. Trans. B.* vol. 185, 1894, pp. 25 & 26.

Roy. Soc. 1897, pp. 48 & 49). And yet he would have us believe that so experienced and careful an investigator as Dr. Forsyth Major had mistaken for the olfactory bulbs structures which are really the optic nerves; in other words, that he has been unable to distinguish in the cranium between the olfactory fossa and the optic foramen! This preposterous charge was made at the Berlin Zoological Congress (Tageblatt, p. 4) and repeated in the later memoir (Anat. Anzeiger, 1902, p. 234) in these words:—  
 “Die von Forsyth Major als Nervi optici gedeuteten Bildungen halte ich für Bulbi olfactorii”; and concerning the true olfactory bulbs and their peduncles, he writes:—  
 “Diese Bildungen scheinen mir darauf zu deuten, dass hier nicht ein Tractus olfactorius von enormer Länge vorliegt, sondern dass hier ein Traktionsdivertikel der Dura mater gebildet wurde, als deren Blutgefässe ich jene Rauigkeiten deuten möchte.”

Such statements as these might be intelligible if they had come from one who had studied only the plaster mould, but Burckhardt visited the British Museum where he had every opportunity for examining not only the original cast, but also the skull from which it was made. That he failed to make use of these opportunities must be evident to anyone who has seen the cranium; for the merest glance is sufficient to show that Dr. Forsyth Major has correctly identified the optic foramina (or canals) and the olfactory fossæ (or rather the common olfactory fossa).

If further confirmation of his statements are wanted, there is in the British Museum a recently acquired skull of a young *Megaladapis* which supplies the desired evidence. This skull, moreover, amply confirms the prediction contained in the following quotation, which was made by Dr. Forsyth Major long before a skull of the young *Megaladapis* was known:—

“When describing the skull of *Megaladapis*, I endeavoured to show that its peculiar low condition is not primitive, but *pseudo-primitive* (Fürbringer), that is to say, that it has been brought about by a ‘retrogressive evolution,’ or a retrograde metamorphosis, if the last term be preferred. If any further proof were needed for this assertion, it would be furnished by the conformation of the brain, as described above, for I trust that no anatomist will maintain that this was the primitive condition in Lemuroids. It may fairly be predicted that, when we come to know the skulls of very young specimens of *Megaladapis*, they will show a much closer approach to the ordinary Lemurid type in the conformation of the brain-cavity and its walls, and the gap between the young and the adult in this respect will prove to be wider than perhaps in any other known Mammal. However, in the Insectivora and most of all in *Centetes*, we find also a very great difference between young and adult in the relative size and conformation of the brain (the brain being even *absolutely* smaller in the old), whilst the least divergence is to be found in Marsupials on the one side, in Man on the other, and this obviously for opposite reasons.”—  
*Proc. Royal Soc.* 1897, p. 49.

I might add that the pattern formed by the sulci in the brain of this young *Megaladapis* is like that of the adult.

The young *Megaladapis* possessed typical Sylvian and postsylvian sulci, and a faintly marked lateral sulcus which extended farther back than it does in the adult.

The plump olfactory bulbs do not project to so great an extent as in the adult; and they are, moreover, separated by a bony septum.

In these respects the young *Megaladapis* more nearly resembles the average Prosimia than the adult does.

The brain of *Megaladapis* must be regarded as the extreme form resulting from those retrogressive changes which affect the brain in all the Prosimiæ. As one of the many indications of this, there is the fact, already emphasized by Forsyth Major, that the brain of *Globilemur* is distinctly larger and much richer in sulci than that of *Megaladapis*, in spite of the fact that the brain of the latter should, in accordance with the laws which regulate the size of the brain, be much the larger, because *Megaladapis* is twice the size of *Globilemur*.

The general appearance of the latter is distinctly pithecoïd, whereas the brain of *Megaladapis* most nearly resembles those Lemurs, such as the Indrisinæ and *Chiromys*, the brains of which are least Ape-like.

#### THE CEREBRAL HEMISPHERE IN *TARSIVUS* AND THE PROSIMIÆ GENERALLY.

The hemispheres of *Tarsivus* assume a peculiar shape, quite unlike that of any other mammal, being flattened in an extraordinary manner. A maximum depth of 10·5 mm.

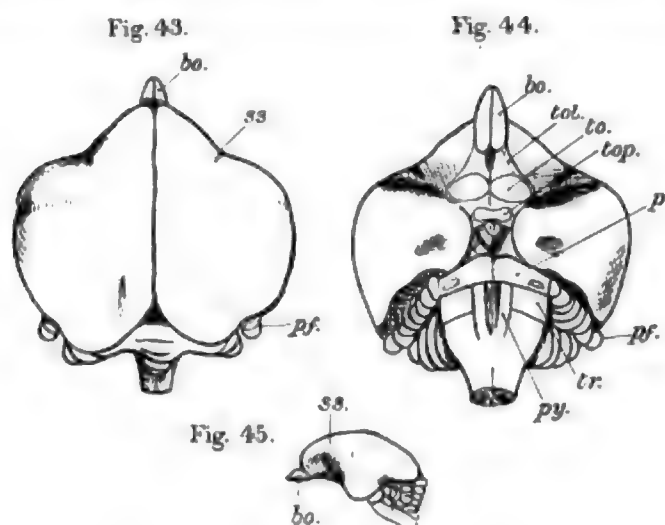


Fig. 43.—*Tarsivus spectrum*. The dorsal aspect of the brain.  $\times 2$ .

Fig. 44.—*Tarsivus spectrum*. The ventral aspect of the brain.  $\times 2$ .

Fig. 45.—*Tarsivus spectrum*. The left lateral aspect of the brain. Nat. size.

in a hemisphere which is 16·5 mm. long and 9·5 mm. broad may seem to stultify this statement; but it is so deeply excavated in part of the region of greatest depth by an unusually extensive orbit and behind it by a deep fossa for the corpora quadrigemina and cerebellum, that it becomes converted into a thin irregular plate.

In a view of the dorsal surface of the brain, the cerebrum hides all the rest of the organ except the caudal margin of the cerebellum and its strongly projecting floccular lobes and olfactory bulbs (fig. 43).

The unusually extensive orbital excavation of the ventral surface of the hemispheres—involving much more than the area usually called “orbital”—gives to the basal aspect of the brain an appearance spuriously resembling that of most birds, in which large eyes



and correspondingly enlarged orbits mould the brain in a manner not unlike that of *Tarsius*. This avian resemblance is still further enhanced by the slender, projecting, olfactory bulbs. [In view of the fact that several well-known writers on cerebral anatomy constantly refer to topographically analogous regions (*e. g.* the occipital "lobe") in the hemispheres of birds and mammals as being homologous, I cannot too strongly insist that any such preposterous suggestions are not intended in the above comparisons.]

Gervais has already pointed out \* that the brain of *Tarsius* approaches nearest to that of the Galagos in form. By reason of the fact that the smaller Galaginæ, such as *Microcebus*, more nearly resemble *Tarsius* in size, it is perhaps not surprising to find an even closer resemblance in the brain-form of the latter two genera. The brain of *Microcebus Smithi* is slightly smaller than that of *Tarsius* †. Although the cerebral hemisphere of *Microcebus* is 1 mm. shorter than that of *Tarsius*, it seems to overlap the cerebellum to a slightly greater extent. The maximum depth of the hemisphere is less than 1 mm. greater in *Microcebus*. Nevertheless the natiform eminence (of the pyriform lobe) appears to form a much more prominent boss in the latter, because it is narrower and its anterior margin forms a right angle with the ventral margin of the anterior part of the pyriform lobe. The smaller eyes and orbits in *Microcebus* lead to a much smaller orbital excavation of the hemisphere, and consequently the shape of the brain is much more like that of the majority of mammals. Each hemisphere of *Tarsius* is about 15 mm. broader (at its maximum diameter) than that of *Microcebus*.

The olfactory bulb is placed almost wholly in front of the hemisphere, and is laterally compressed as in the Galaginæ (especially *Microcebus*) and the Lorisinæ. In both of these respects it differs markedly from the Lemuriniæ, Indrisinæ, and *Chiromys*, in which the bulb is flattened dorso-ventrally and overlapped by the cerebral hemisphere. In *Tarsius* the bulb presents a triangular outline in profile, its anterior extremity forming an acute angle. Its size would be regarded as very small in any other Order of mammals. A comparison of the size of the bulb with that of *Microcebus* (which in this respect may be regarded as typical of the Prosimiæ) shows that the olfactory bulb is less than half as large as it is in the Lemurs.

The olfactory peduncle is short and broad, as it is in all the Prosimiæ and in most mammals excepting the Apes. Like that of the latter, however, and unlike that of most mammals, the lumen of the peduncle and bulb is obliterated in *Tarsius* and other Lemurs. The short peduncle of the olfactory bulb becomes continuous with a small pyriform lobe, which is placed wholly on the ventral surface of the hemisphere, forming approximately the mesial third of the great orbital depression. The rhinal fissure is almost completely obliterated, as is the case in most Lemurs and, among small mammals, the Chiroptera. But its situation is clearly recognizable by the difference in the appearance of the surfaces of the pyriform lobe and the neopallium, and in one hemisphere a shallow furrow remains to indicate its position. There is a small tuberculum olfactorium presenting features such as are common to all mammals.

In spite of the small size of the olfactory bulb, the hippocampus is relatively larger

\* Journ. de Zoologie, tome i. p. 23.

† In this statement I refer only to the specimens in my possession.



than in the Apes, but smaller than that of the other Lemurs. Although the hippocampus is an appendage, so to speak, of the apparatus of smell and dwindles almost to nothing in smell-less animals, like the Odontoceti, the size of the hippocampal formation does not seem to vary directly (as that of the pyriform lobe does) with the degree of osmatism. The hippocampus is distinctly larger in all Lemurs than it is in the Apes, and *Tarsius* shares this peculiarity of the Lemurs, although in a lesser degree than the other Lemurs. Thus, if we compare the hippocampal swelling in the lateral ventricle of *Tarsius* with that of *Hapale* (the Ape which most nearly approaches it in size), we cannot fail to be struck with the contrast between its plump columnar form in the Lemur and its slender proportions in the Ape.

The most that can be seen of the mammalian hippocampal formation in a mesial view of the hemisphere is a strip of fascia dentata and fimbria, and a variable area of alveus-covered "inverted hippocampus\*." In *Tarsius* the fascia dentata and fimbria form two bands of equal and uniform breadth, not separated by any "inverted hippocampus." These bands extend almost vertically upward, with only a very slight inclination forward, and the fascia dentata passes directly to the splenium of the corpus callosum, without the formation of any subsplenial flexure. Such a phenomenon does not occur elsewhere among the Lemurs, but we find a parallel in the case of the Sloths†, in the brain of which there is, as in *Tarsius*, an unusually short corpus callosum. This is indicative of a very primitive state.

The supra- and pre-callosal vestiges of the cephalic extension of the hippocampal formation call for no special mention, because in *Tarsius*, as in all Primates, these structures are extremely insignificant and difficult to demonstrate. The hippocampal tubercle is relatively large in *Tarsius*, seeing that it involves about one third of the length of the hippocampal formation.

The corpus callosum is remarkable (in an Order in which this commissure is distinguished for its great length) in being unusually short. It measures only 5.5 mm. in a hemisphere 17 mm. long, whereas the corresponding proportions in a *Lemur mongoz* are 17.5:39, in a *Nycticebus tardigradus* 14:34, and in a *Chiromys* 22:45. Its thickness is remarkably uniform throughout, the splenial and genual extremities being only very slightly thicker than the body, whereas in *Lemur* and most of the Prosimiae the splenium and genu are twice or even three times the thickness of the body. The corpus callosum is also more obliquely placed than it is in *Lemur*. It exhibits a very slight, regular, dorsally-directed convexity, and its slightly dependent anterior extremity shows no sign of being bent backward to form a rostrum, such as we find in the Apes. In all these respects the brain of *Tarsius* approximates to the primitive condition exhibited in the Insectivora.

In consequence of the relatively slight backward extension of the corpus callosum, the psalterium or hippocampal commissure is short and plump. In all other Prosimiae, as in most mammals, the great bulk of the psalterium is collected at the upper end

\* *Vide* Journ. Anat. and Phys. vol. xxxii. 1897, pp. 30 & 31.

† "Brain in the Edentata," Trans. Linn. Soc. ser. 2, Zool. vii. 1899.

of the lamina terminalis just above the anterior commissure, and is linked to the ventral surface of the splenium of the corpus callosum by a thin attenuated band, composed of scattered commissural fibres. In the Hapalidæ these scattered fibres are wanting, so that the psalterium is separated from the corpus callosum by a wide gap\*. In *Tarsius* there is little or no attenuation of the dorso-caudal part of the psalterium. A parallel for this is found in the brain of the Bradypodidæ.

There is a septum lucidum composed of two thin sheets enclosing between them a cavum septi, which is freely open below in the wide interval between the genu of the

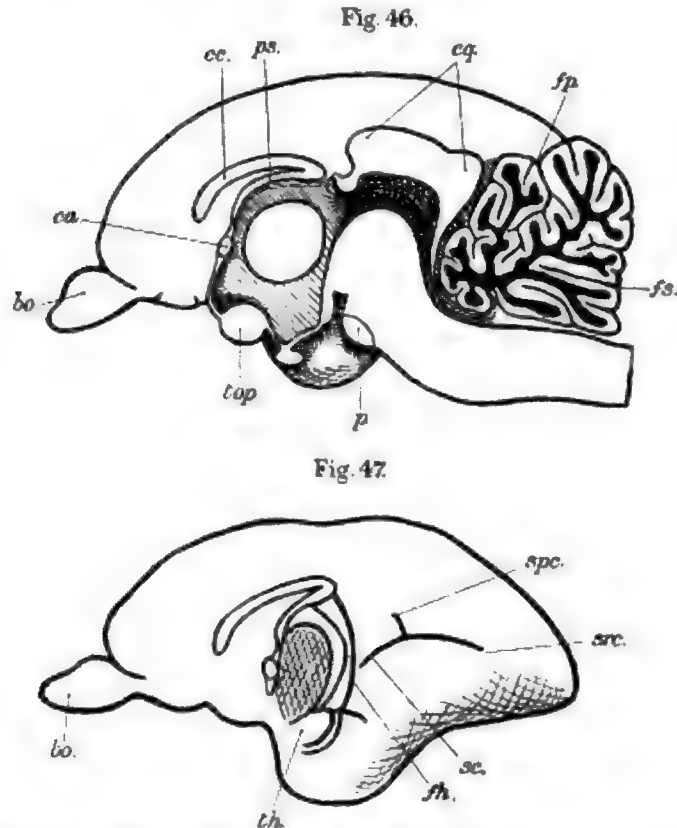


Fig. 46.—*Tarsius spectrum*. Surface exposed by a mesial sagittal section.  $\times 4$ .

Fig. 47.—*Tarsius spectrum*. Diagram representing the mesial surface of the right cerebral hemisphere.  $\times 4$ .

corpus callosum and the psalterium. In spite of a very generally-expressed belief to the contrary, this is the condition which prevails in the vast majority (practically in all) of the Eutheria.

The anterior commissure is slightly more than 1 mm. deep and just less than 1 mm. thick (in the horizontal plane). For a Primate of such small dimensions, these measurements must be regarded as large, and especially so when it is recalled that *Tarsius* is the most microsmatic of Lemurs, and therefore the individual in which such a phenomenon would *à priori* be least expected. This means that the neopallial element in the

\* Vide Journ. Anat. and Phys. vol. xxxii. 1897, fig. 23. p. 51.

commissure is relatively large. And this is yet a further indication of the primitive state of the brain of *Tarsius*.

The anterior part of the mesial surface of the hemisphere is quite smooth and flattened against the corresponding surface of the other hemisphere. This flattened area, prolonged backward above the corpus callosum, extends for more than 6 mm. in the caudal direction beyond the splenium of the corpus callosum as a band less than 3 mm. wide. The whole of this flattened area is entirely devoid of sulci, no trace of the intercalary (calloso-marginal), genual, or rostral sulci, which are found in some Lemurs, being detected here. Ziehen says \* that in the region above the corpus callosum there is a deep furrow on the mesial surface, which is probably *not* a vascular groove, but is a true fissure running parallel to the corpus callosum. In all of the four hemispheres of *Tarsius* which I have examined this so-called sulcus  $\alpha$  of Ziehen is nothing else than the impression of the anterior cerebral artery, as it obliquely crosses the surface of the hemisphere, after having bent around the genu of the corpus callosum. A similar impression may be found in any mammalian brain, as I have already pointed out in the case of *Ornithorhynchus* †.

In a cerebral hemisphere 17 mm. long, 8 mm. (or almost half of its length) lies behind the splenium of the corpus callosum. Such a marked caudal or (as it is commonly called) occipital extension of the hemisphere is found nowhere else among the Lemurs, and a parallel for it must be sought among the Apes, where such an exaggerated backward prolongation is present in the Hapalidæ and the smaller Cebidæ. It is a significant fact that this Pithecoïd condition is found in a brain which in many other respects exhibits more primitive features than the majority of the Prosimiæ. We have already seen that a narrow upper strip of this postsplenial area of the mesial surface is flattened against the corresponding surface of the other hemisphere. The rest of this region is deeply excavated in a very irregular manner in adaptation to the shape of the corpora quadrigemina and cerebellum, which are partly overlapped by the occipital prolongation as by a cap.

Immediately below (or to the lateral aspect of) the flat area there is a deep cup-shaped depression about 3 mm. in diameter, placed about 2 mm. behind the splenium. This is produced by the anterior quadrigeminal body. In this depression there is a triradiate arrangement of deep sulci diverging from its centre. The calcarine sulcus extends downward and forward toward the hippocampal fissure; the retrocalcarine extends horizontally backward; and the paracalcarine extends upward, but does not quite reach the flat area. The other two sulci, however, just manage to cross the rim of the cup-shaped depression.

By comparison with other Prosimian brains, it will be shown later on that the sulci  $\alpha$  and  $\gamma$  probably represent the true calcarine sulcus (*i. e.* that called "anterior calcarine" by Cunningham), and that the sulcus  $\beta$  is the retrocalcarine (Cunningham's "posterior calcarine"). All of these sulci are very deep and completely involute the mesial wall of the very large pithecoïd posterior cornu of the lateral ventricle. In other

\* Archiv f. Psych. Bd. xxviii. p. 1810.

† "Further Observations on the Brain in the Monotremata," Journ. Anat. and Phys. vol. xxxiii.

words, there is formed a calcar avis of such great proportions as to closely resemble in shape and size that of the smaller Apes. This calcar is larger than that of the other Prosimiae, although the condition found in the Galaginae nearly approaches it.

It is noteworthy that in Ziehen's memoir on the Lemur's brain this calcarine sulcus—the only true sulcus found in the brain—is entirely ignored, although reference is made to a large number of spurious sulci. If this significant sulcus had really been absent, as Ziehen's account would lead one to suppose, this would have placed the brain of *Tarsius* in a category quite apart from that of all the other Lemuroidea (and in fact all Primates), instead of adding yet another convincing testimony to the close Prosimian affinities of *Tarsius*.

About midway between the calcarine sulcus and the ventral border of the hemisphere there is a very deep irregular notch extending backward on to the caudal margin of the hemisphere. When the brain is *in situ* in the skull, this deep depression is occupied by the bony case of the strongly projecting floccular lobe of the cerebellum.

Ziehen\* represents two separate depressions in this situation: one on the mesial surface, which he refers to as  $\beta$ , and the other he calls "die Einbuchtung der unteren Contours des Temporo-occipitallappens." They are obviously both parts of the one floccular fossa. Although when describing the *Tarsius*-brain Ziehen inclined to the view that the sulcus  $\beta$  is merely a depression caused by a bony projection, yet in the same memoir we find this writer discussing which of two sulci in the hemisphere of *Nycticebus* (p. 906) represents the "sulcus  $\beta$  in *Tarsius*"! Then he adds, "Am wahrscheinlichsten ist mir, dass  $\beta$  wenigstens z. Theil auch dem Vereinigungspunkt von  $\rho$ ,  $\sigma$ , und  $\pi$  [the calcarine group of sulci] entspricht." If this suggestion is correct, Ziehen's drawing (fig. 2, p. 900) is very misleading and erroneous, for the relationship of his sulcus  $\beta$  to the floccular fossa (his "Einbuchtung") is very different to that of the true calcarine sulcus.

Just below the retrocalcarine sulcus there is in one of my specimens a shallow horizontal furrow, which crosses on to the caudal margin of the hemisphere. As it is very shallow and lodges a branch of the posterior occipital artery, it is possible that it is caused by the latter. In neither hemisphere of my second specimen is there any such sulcus.

The narrow cleft between the optic chiasma and the tuberculum olfactorium, which contains the representative of the locus perforatus of other mammalian brains, is prolonged transversely outward across the pyriform lobe as a vallecule Sylvii. Opposite the outer end of the latter a furrow extends outward (upward) and slightly forward across the orbital excavation of the hemisphere, which it divides into two approximately equal parts. It occupies the situation of and probably represents the Lemurid Sylvian fissure. It does not extend so far up as the dorsal lip of the orbital excavation, so that it is not visible on the dorsal surface, although an indentation of the margin (fig. 43) indicates its situation. A comparison with the condition found in *Microcebus* shows that this must represent the Lemurid Sylvian or suprasylvian sulcus. When we remember that the area which is usually called "orbital surface" lies wholly in front of the

\* Arch. f. Psychiat. xxviii. 1896, p. 900.

Sylvian fissure in other brains, it will be seen that the position of this "Sylvian fissure" in *Tarsius* is very peculiar. The further discussion of the significance of this furrow will be more intelligible if it be postponed until the nature of the Sylvian fissure of the other Lemurs has been considered.

Apart from this sulcus, the rest of the cranial aspect of the hemisphere is smooth and devoid of sulci.

There is a very slight flattening, unworthy of the name of furrow, just behind and parallel to the caudal margin of the orbital excavation. It may possibly represent the postsylvian sulcus.

An even slighter flattening is found parallel to the mesial plane in a situation where the intraparietal (lateral) sulcus is found in other Lemurs.

In view of the considerable differences which are shown to exist by comparing the brains of various Lemurs, the resemblance between the brains of *Tarsius* and the smaller Galaginæ is a fact of considerable significance. The peculiar features of the calcarine group of sulci so strikingly reproduce those found in all the other Prosimiæ, and in no other mammals of a similar size (with the possible exception of the Edentate *Manis*), that they alone constitute an important indication of the closeness of the bond of affinity which unites *Tarsius* to all the other Lemurs.

It is also peculiarly instructive to note that the chief differences between the brain of *Tarsius* and the other Lemurs occur in the commissural region; and in respect to this *Tarsius* approximates much more nearly to the primitive mammalian type than do the other Prosimiæ.

As in *Microcebus*, *Tarsius* possesses only one sulcus other than the calcarine group (and, of course, the hippocampal fissure). This other sulcus is the Sylvian or, perhaps, its suprasylvian element. In these respects these small Prosimian brains resemble those of the lowlier Apes.

In *Galago* small lateral and orbital sulci make their appearance on the outer aspect, and intercalary and rostral sulci on the mesial surface. In the Great Galago the lateral sulcus becomes longer, and a coronal sulcus makes its appearance; the sulcus *f* and the postsylvian furrows also may become developed.

In the larger Lemurs diagonal, postlateral, collateral, and other furrows may develop.

#### THE BRAIN-STEM.

By this term I mean those parts of the brain which remain after removing the cerebral hemispheres and cerebellum.

In my Memoir on the Brain in the Edentata I pointed out that these parts are subject to much less variation in the different mammalian Orders than are the cerebral hemispheres and cerebellum. A careful study of these regions in *Tarsius*, *Lemur*, *Microcebus*, and, by macroscopic means only, in *Chiromys*, *Galago*, and several other Prosimiæ, has revealed no features which are not equally peculiar to all mammals, so that no lengthy consideration of these regions is necessary.

There is practically nothing concerning these parts of the brain in the literature of

the Prosimiæ, for the few writers \* who refer to any region other than the cerebral hemispheres do not record anything worth recalling in reference to the brain-stem.

There is nothing in the walls of the third ventricle, the pineal body, the ganglion habenulæ, the habenular commissure (commissura superior), the hypophysis, corpora mammillaria, the interpeduncular ganglion, the crura cerebri, pons Varolii, and corpus trapezoidea to distinguish them from the great majority of mammals and from the smaller Apes. Many of the structures enumerated in this list are found to be considerably modified in Man and the higher Apes in comparison with the majority of mammals. Thus the corpus trapezoides becomes gradually covered by the pons Varolii; the interpeduncular ganglion becomes deeply buried between the crura cerebri and pons, and is unrecognizable as a distinct ganglionic mass; the corpora mammillaria become more distinctly separated the one from the other. But these changes occur in the transition from the smaller to the larger Apes, and hence it is not surprising that, like the former, the Lemurs should preserve the common mammalian features.

There are only three features of the Prosimian brain-stem that call for special note. These are the relative size of the corpora quadrigemina; the proportions of the optic thalamus and its external (anterior) geniculate body; and the olivary body in the medulla oblongata.

The general features of the corpora quadrigemina are remarkably constant in all the Meta- and Eutheria. The features which are subject to most variation are the relative proportions of the two pairs of colliculi or quadrigeminal bodies, and the size of the tractus peduncularis transversus.

Gustav Retzius has recently published some excellent representations of this region in the brains of *Homo*, *Anthropopithecus*, *Simia*, *Ursus*, *Lutra*, *Phoca*, *Bos*, *Equus*, *Oris*, *Sus*, *Lepus*, and *Macropus* †; Ziehen has described its features in the Marsupialia and Monotremata ‡; and I have briefly described its appearance in the Edentata § and Monotremata ||. Since then I have carefully examined this region in representatives of every mammalian Order with the special purpose of comparing it with the Prosimian mesencephalon. The most important result of this study is graphically demonstrated in the accompanying series of diagrams, which represent the dorsal aspect of the thalamic and mid-brain regions in *Lemur*, *Tarsius*, and a heterogeneous collection of mammals including *Cercopithecus*, *Felis*, *Procapra*, *Lepus*, *Dasypus*, and *Macroscelides*, which represent every phase of the changing proportions of these bodies in the whole Mammalia. All the diagrams are magnified in the same degree.

The most striking feature of the diagram representing the condition in *Lemur* is the relatively enormous size of the optic thalamus and the smallness of the corpora quadrigemina. As we descend the mammalian scale there is a progressive diminution in the

\* Burmeister (*Tarsius*), Owen (*Chiromys*), Milne-Edwards (Indrisine), Oudemans (*Chiromys*), and Flatau and Jacobsohn (*Lemur macaco*).

† Biolog. Unters., N. F. Bd. viii. no. 5, Taf. 16 & 17.

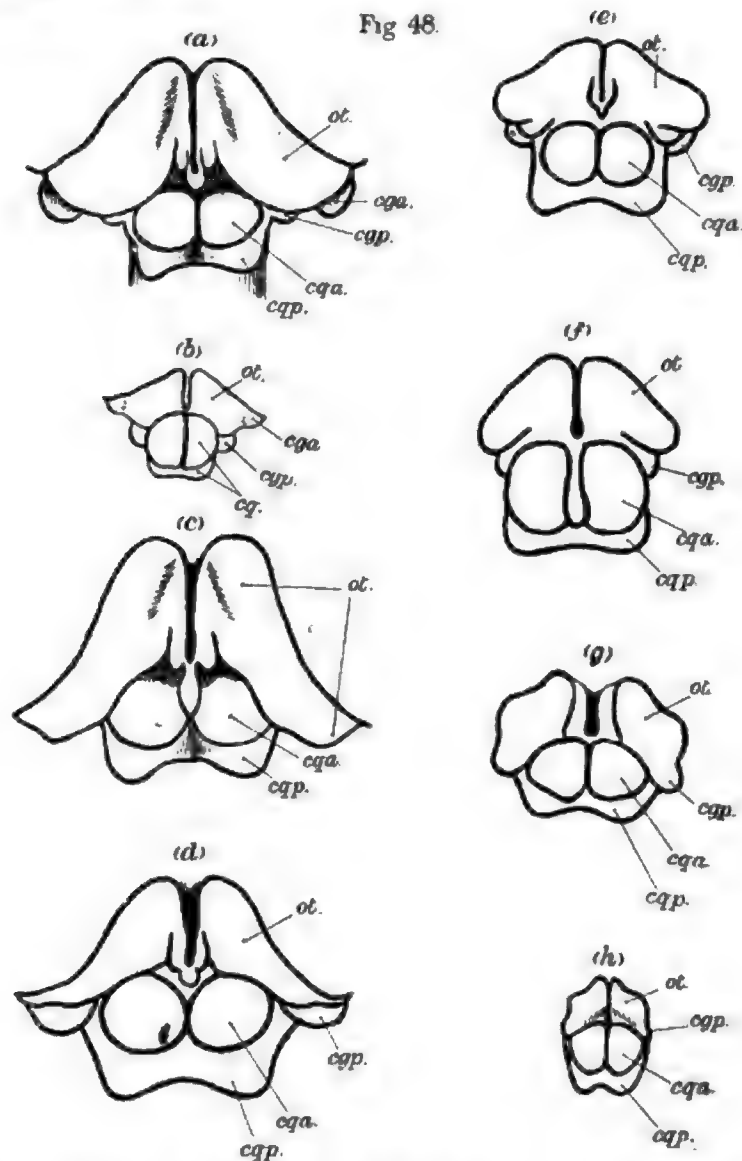
‡ Jenaische Denkschrift, 1897.

§ Trans. Linnæan Soc. ser. 2, Zool. vol. vii. 1899.

|| Journ. Anat. and Phys. vol. xxxiii.



size, both absolute and relative, of the optic thalamus. In the lowly Metatheroid Insectivore *Macroscelides* the dorsal area of the thalamus is little if any bigger than the anterior quadrigeminal body.



A series of diagrams representing the dorsal surface of the thalamic and mesencephalic regions in (a) *Lemur*, (b) *Tarsius*, (c) *Cercopithecus*, (d) *Felis*, (e) *Procyon*, (f) *Lepus*, (g) *Dasypus*, and (h) *Macroscelides*. All magnified 2 diameters.

In these respects *Lemur* distinctly conforms to the peculiar condition of the Primates, and differs most markedly from all other mammals.

It is equally significant that in a large-eyed mammal like *Lemur* the anterior quadrigeminal bodies are so small as they are, not only relatively, but absolutely. They are certainly much bigger in *Tarsius*, but in this creature the eyes attain such exceptional dimensions.



In *Lemur* (and all the Prosimiæ) the lateral (anterior) geniculate body becomes much larger and more distinct than it is in most mammals: and this feature it also shares with the other Primates.

It might perhaps be imagined that the larger dimensions and more distinct separation of the lateral geniculate body from the rest of the thalamus are due to the fact that the optic tracts are unusually large in all the Lemurs. But this cannot be the whole explanation, because in many other large-eyed mammals (see many Rodents, Ungulates, and others) there is no such distinctness of the external geniculate body as we find in all Lemurs and other Primates. This phenomenon must be due to an increased perfection of the cortical path for visual impulses, rather than to a mere enlargement of the lower optic tracts.

The four quadrigeminal bodies rise to the same level, and resemble in shape those of the Myrmecophagidæ more nearly than those of any other mammals (excepting the other Primates). There is a well-defined tractus peduncularis transversus, but it calls for no further mention.

If the region of the medulla oblongata in the Lemurs be compared with that of other mammals of a corresponding size, the only noteworthy distinctive feature of the former will be the relatively greater prominence of the olivary body. It is, however, somewhat smaller and less prominent than it is in most Apes, the chief olivary nucleus being smaller in proportion to the internal accessory olivary nucleus in the Lemurs than it is in the Apes.

#### THE CALCARINE SULCUS AND THE OCCIPITAL PROLONGATION OF THE HEMISPHERE.

The foregoing notes will have made it clear that a triradiate group of three sulci—which I have called calcarine, retrocalcarine, and paracalcarine respectively—form an arrangement which presents identical features in ALL the Prosimiæ. No one has ever questioned the identity of the furrow labelled calcarine with the sulcus so-called in the Apes. The sulcus which I have distinguished by the name “paracalcarine” is regarded by most writers as the representative of the parieto-occipital sulcus in the Apes. Flower was, I believe, the first to suggest this view; but afterwards renounced it in favour of the hypothesis that the paracalcarine sulcus represents one of the limbs of bifurcation which the calcarine sulcus presents in most Apes. When I began writing this memoir I subscribed to the latter view, chiefly because the parieto-occipital sulcus is absent in several of the lowlier Cebidæ and all of the Hapalidæ; and it seemed therefore to be a furrow which becomes evolved in the Apes: but in developing the argument which is here unfolded, I became convinced that there may be another and more probable way of regarding this matter. None of the writers who call the paracalcarine sulcus “parieto-occipital” seem to have considered the possibility of it being any other furrow.

Recognizing the identity of the calcarine sulcus in all the Primates, we may pass on to the consideration of its relationship to the lateral ventricle, with a view to determine

if there be any qualitative difference in the nature of the occipital prolongation of the hemisphere in Lemurs and Apes. For the extent of this region of the hemisphere, or, rather, its relation to the cerebellum, is commonly supposed to be a feature of the utmost importance as an index of cerebral development, even by writers who have devoted much labour to the study of this part of the brain.

This will lead not unnaturally to the enquiry as to whether the calcarine sulcus is found in any mammals other than the Primates.

The most conflicting statements are found in the literature (quoted earlier in the notes) regarding the posterior cornu of the lateral ventricle.

Burmeister (1846) described an extensive diverticulum of the ventricle in *Tarsius*, and about the same time Vrolik denied its presence in *Nycticebus* [*Stenops*]. Both of these statements are true.

In 1862 Flower thought that he had found a posterior cornu and calcar in *Lemur fulvus* [*nigrifrons*] and also in a *Galago* of unknown species; but while his monograph was being revised in proof he became sceptical and added in a footnote: "A further examination of this specimen [a brain of *Galago* in the Museum of the Charing Cross Hospital], and of the brains of some allied genera, leads me to doubt whether the above described 'cavity' in the posterior lobe existed before dissection, the length of time that it had been in spirit having greatly facilitated this process. If it did not, it will justify the statement of the absence of the hippocampus minor by anatomists who have looked at this structure only in its relation to the posterior cornu, but at the same time will afford a further illustration of what I have endeavoured to show . . . viz. :—that the part of the brain to which this term [calcar] has been applied can exist independently of the ventricular cavity" (Phil. Trans. 1862, p. 198, footnote). I have quoted this very interesting and luminous note in full, not only by reason of its important bearing upon the question at issue, but also to express surprise that its author should have suddenly stopped on the way to the full interpretation of the morphology of the calcar and calcarine sulcus, and have categorically denied its existence in the Cat's brain, after thus removing all the obstacles to such an obvious inference as to the identity of the so-called "splenial" sulcus in the Cat and the Prosimian calcarine. In the same year he wrote a second memoir [which, however, was not published until 1866 (Trans. Zool. Soc. vol. v.)], in which he makes the statement that it is impossible to determine whether or not the posterior cornu exists in *Nycticebus tardigradus* [*Stenops javanicus*] (p. 106).

In the memoir on the brain of *Chironomys*, which was published in the same year (Trans. Zool. Soc. vol. v.), Owen seems to represent a small posterior cornu (in fig. 5). This fact is all the more significant if it is intentional, as the author was engaged at the time his memoir was written in a heated controversy, in which he maintained that the posterior cornu and the calcar were human characteristics.

In Milne-Edwards's contribution to the History of Madagascar ((2) tome vi. 1876, p. 206) the author refers to Flower's demonstration of the existence of a calcar in *Lemur* and *Galago* (quoting Phil. Trans. 1862, p. 197), and states that he has confirmed this in the case of the forms studied by Flower, but denies its (calcar's) existence in *Indris*,

*Propithecus*, and *Arahis*. The writer has apparently overlooked Flower's footnote (quoted above) which clearly shows that a posterior cornu is not necessary to the existence of the calcar. The latter must be present in the Indrisinæ (because a calcarine sulcus occurs in this subfamily as it does in the Lemurinae) even though the posterior cornu may be absent. For this is obviously what the author means to imply. His other statements regarding the posterior cornu and calcar avis (on p. 205) are contradictory and their meaning is not altogether clear.

The only other writers (so far as I am aware) to refer to the posterior cornu in the Lemurs are Flatau and Jacobsohn ('Handbuch,' p. 189); and as they have obviously not read any of the literature quoted above (excepting Burmeister's remark concerning *Tarsius*) they dismiss this, the most crucial feature of the Prosimian brain, in that casual manner, which is unfortunately the rule rather than the exception in their barren and misleading work. Thus they dispose of the whole question in the case of *Lemur macaco* in the words:—"Der Seitenventrikel ist bei den Halbaffen von gleicher Beschaffenheit, wie bei den wahren Affen und auch von den gleichen Gebilden begrenzt" (p. 189), as though there were no problem to be settled. Moreover it will be shown that this observation is misleading, if not quite erroneous. The only other Prosimian brain which the authors examined was one which they label "*Stenops gracilis*," but which obviously belongs to "*Nycticebus tardigradus*." Now although the interesting problem as to the existence or absence of the posterior cornu in this genus had been definitely raised and left unsettled (*vide supra*) by Flower (whose numerous and important contributions to the Comparative Anatomy of the mammalian brain these writers of a text-book on this subject almost wholly ignore), Flatau and Jacobsohn merely state (in the paragraph corresponding to that quoted above regarding *Lemur*):—"Die übrigen Verhältnisse am Gehirn des *Stenops* sind so ähnlich denen am Gehirn des Maki, dass eine besondere Besprechung unnötig erscheint" (p. 199). But, as in the case of *Lemur*, they give tables of measurements, among which figures "Abstand der vorderen Spitze des Vorderhorns vom hinteren Pol des Hinterhorns" (pp. 199 and 189) \*.

Ziehen, Beddard, and all other recent writers do not even so much as refer to the subject.

After carefully examining the specimens concerning which the above-quoted statements of Flower's were made, I felt convinced that an undoubted patent posterior cornu exists in the genus *Lemur*. I subsequently made dissections of the brains of *Nycticebus*, *Microcebus*, *Tarsius*, and two other specimens of *Lemur*, all of which had been in preservative solutions for long periods; and the results seemed to confirm my earlier conviction. But recently I examined the fresh brain of a *Lemur fulvus*, and, to my great surprise, found *no trace of any patent posterior cornu*. Since then I have been unable to find any posterior cornu in three other fresh brains of various species of *Lemur* and a fresh brain of *Nycticebus*. In view of these unquestionable facts, and of the

\* This reference to a "Hinterhorn" is, however, meaningless, for they use the term in referring to the brain of all mammals.

equally decisive remarks of Milne-Edwards\*, and Flower's hesitation in adopting the view which seemed so obvious, one naturally becomes sceptical of the existence of such a ventricular diverticulum in any Prosimian brain.

If a horizontal section be made through the cerebral hemisphere of any Lemur so as to pass just below the level of the corpus callosum, the pericalcarine region will present the appearance represented in the figures 49 (*Nycticebus*) and 50 (*Lemur fulvus*). The hippocampus is prolonged mesially into continuity with a long pallial folium, which extends almost as far as the mesial plane and then becomes sharply bent upon itself so

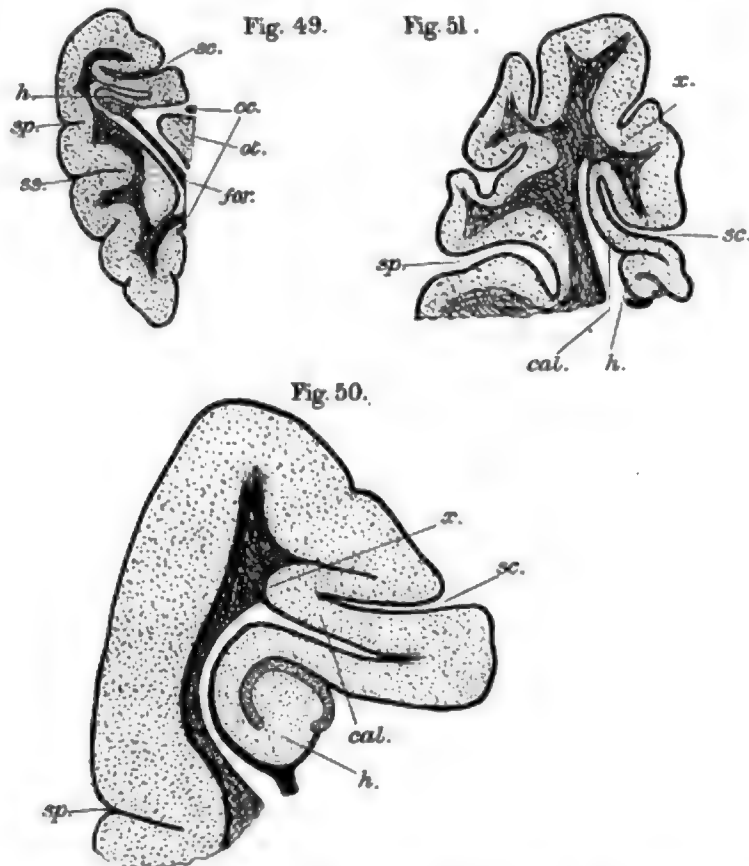


Fig. 49.—*Nycticebus tardigradus*. Horizontal section through the cerebral hemisphere immediately below the corpus callosum.  $\times 2$ .

Fig. 50.—*Lemur fulvus*. Part of a corresponding section.  $\times 4$ .

Fig. 51.—*Cercopithecus sabaeus*. A corresponding section.  $\times 2$ .

as to form the slightly oblique anterior wall of the deep calcarine sulcus. At the bottom of the calcarine sulcus the pallium again becomes acutely flexed and forms the posterior lip of the calcarine furrow. It is of the utmost importance to recognize at this stage that the anterior wall of the calcarine sulcus forms a part of the boundary

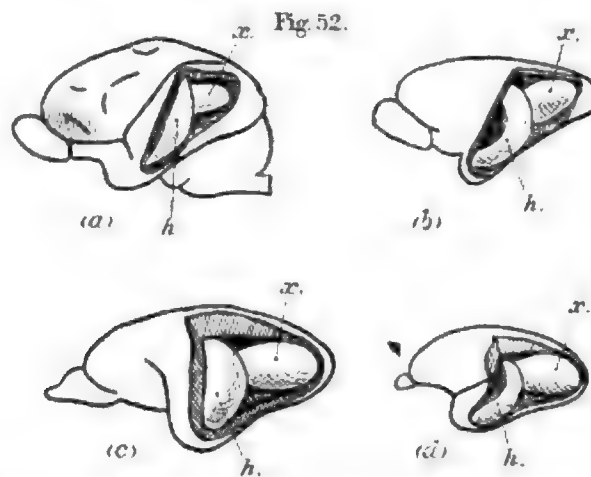
\* Only so far as the Indrisinae are concerned; for, in view of these results of my recent re-examination of the genus *Lemur*, I fail to understand the significance of Milne-Edwards's reference to this genus (*vide supra*).

of the lateral ventricle, its medullary layer being part of the ventricular lining; whereas the posterior wall of the sulcus is far removed from the ventricle, and its medullary layer is not free but is fused to the general medullary mass of the hemisphere.

No part of the pallial lining of the retrocalcarine and paracalcarine sulci takes any direct share in forming the walls of the lateral ventricle.

If we next examine a similar section in the cerebral hemisphere of an Ape, such as *Cercopithecus* (fig. 51), essentially the same state of affairs is revealed. The posterior wall of the calcarine sulcus is far removed from the ventricle and its medullary layer is fused to the general medullary mass.

As the result of the greater obliquity of the calcarine sulcus and of the smaller size of the hippocampus, a much larger area of the anterior (or lateral, as it has now become) wall of the calcarine sulcus is exposed in the ventricle and forms the "calcar avis." The only difference between the conditions in the Lemur and the Ape is a quantitative and not a qualitative one. As the result of the larger dimensions of the neopallium, the



The left cerebral hemisphere of (a) *Nycticebus*, (b) *Microcebus*, (c) *Tarsius*, and (d) *Haplorhina*, dissected to show the hippocampus and the calcarine eminence (x) [not the true calcar in a and b].

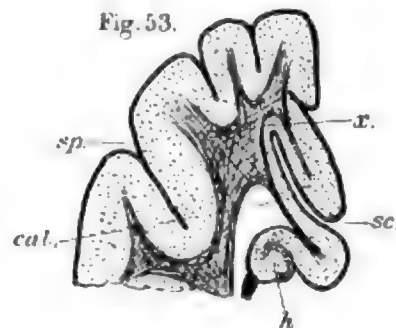
hemisphere has extended further backward and has produced a posterior diverticulum of the lateral ventricle, in the mesial wall of which the calcar is found. In the Lemur the homologue of the calcar is also found, even though there is no posterior cornu of the ventricle, but it faces the alveus of the hippocampus, so that no bulging calcar can be seen when the ventricle is opened.

If the lateral wall of the hemisphere be dissected away in the brain of a *Lemur* which has been toughened in some preservative fluid, a line of cleavage readily extends backward from the posterior angle of the ventricle between the dense medulla of the calcarine cortex and the looser medullary matter in contact with it; in this way the observer can readily be deceived into the belief that a posterior cornu exists and that a rounded calcar (fig. 50, x) projects into it. The region x, however, is not the homologue of the true calcar, as a comparison of figs. 50 and 51 will at once show. The appearance of the "calcar," so exposed in the brains of *Nycticebus*, *Microcebus*,

*Tarsius*, and *Hapale*, is shown in the accompanying drawings (fig. 52). In *Tarsius* and *Hapale* the swelling exposed is partly and perhaps wholly a true calcar, like that of *Cercopithecus*.

In the brain of the Apes, as also in Lemurs, the walls of the paracalcarine and retrocalcarine sulci do not come into relationship with the ventricle.

If next we practice a corresponding section in the brain of a Dog (fig. 53), a state of affairs is exposed which is either identical with that of the brain in the Primates or presents the closest resemblance to it. Immediately to the caudal side of the hippocampus the neopallium behaves in the same manner as it does in the brain of Lemurs and Apes; but the *deep, oblique* sulcus is not usually called "calcarine," but



*Canis familiaris.*

A section analogous to those represented in figs. 50 and 51.  $\times 2$ .

by Krueg's title "splenial." A glance at this figure will at once show that, unless there be some overwhelming argument to the contrary, we must regard this part of the splenial sulcus of the Dog as the representative of the calcarine sulcus of the Primates. It is commonly argued that there can be no calcarine sulcus in the Carnivora because there is no posterior cornu; but the same writers do not deny the calcarine nature of the analogously-placed furrow in the Lemurs, even though there is no posterior cornu there. We may therefore, at any rate as a working hypothesis, refer to this part of the Dog's splenial sulcus by the name "calcarine." Now the conditions which are found in the Dog also prevail in every Carnivore, without exception. It is therefore very surprising to find Flower speaking of "the absence of anything resembling the calcarine sulcus" in the Cat's brain in the same memoir in which he made the important observation (quoted above) that the existence of a patent posterior cornu is not a necessary condition of the presence of a calcar, and therefore of a calcarine sulcus. Even if the calcarine sulcus should ultimately prove to be not homologous with any part of the splenial furrow, it is clearly erroneous to say that the latter does not "resemble" it. In the case of certain Carnivores, such as the Seals, a definite posterior cornu of the ventricle is found, and in some cases, e. g. *Phoca*, it reaches large dimensions: in these animals the "splenial bulging" in the lateral ventricle so closely "simulates" the "calcar" of the Primates that there can be no reasonable doubt as to their identity. This fact was well known early in the last century, for Serres's observations, that "the hippocampus minor [calcar] has hitherto been observed only in Man," which continue "... I have,



however, found it in the Apes and Seals [chez les Singes et les Phoques]”\*, gained a wide currency in the text-books of the period †, and have even persisted in certain French treatises up to the present day. And yet this important fact has been wholly ignored in the discussion of the possible homologues of the calcarine sulcus in other mammals.

[In making this statement I am not unmindful of the fact that in the memoirs of Murie on the brain in the Seals and in the Manatee an anthropocentric nomenclature is adopted and a furrow on the surface of the hemisphere is called “calcarine”; Murie also describes a posterior cornu and a calcar in *Otaria* and *Manatus*.]

The calcar was rediscovered and described in the brain of the Seals by Fish in 1898; but this writer so signally failed to appreciate the morphology of this region of the brain as to entertain a doubt as to whether the sulcus, which produced this calcar, ought to be regarded as the calcarine or the parieto-occipital! ‡. He makes the following quotation from Wilder’s “Anatomical Technology” :—“Between the ordinary Carnivora and the Monkeys are two groups whose brains should be studied with especial care; the Seals have a rudimentary postcornu and occipital lobe, and these parts are said to be developed in the *Lemurs* which have affinities with both the Carnivora and the Primates” (p. 80).

Although Fish quotes the statements of Tiedemann, who represents *Phoca* as lacking a posterior cornu, he appears to be ignorant of the above-quoted observation of Serres, in spite of its wide currency in such works as those of Cuvier, Leuret and Gratiolet, and Topinard. His suggestion that the splenial sulcus of the Pinnipedia may possibly represent the parieto-occipital sulcus becomes all the more amazing when he makes such definite statements as :—“[*Phoca*] shows a postcornu relatively as large or larger than in the primate brain, with a distinct calcar or hippocampus minor in which a portion of the splenial appears as a total fissure” (p. 88).

I have confirmed all these statements of fact in the Seals and prepared a dissection of this region in *Phoca* for the Museum of the Royal College of Surgeons (Specimen D. 377, Physiological Series).

Since Krueg carefully described and named the “splenial” sulcus in a large number of Carnivores and Ungulates, no one has questioned the identity of the furrows so-named in the two Orders. The different position of the furrow on the hemisphere in the Ungulata modifies its obliquity so that it does not so closely resemble the calcarine sulcus in the Primates as that of the Carnivora does. Nevertheless the relationship of its two walls to the lateral ventricle and its depth (in comparison with neighbouring sulci) would suffice to show its identity, even if we were not acquainted with its

\* ‘Anatomie Comparée du Cerveau,’ Paris, 1826, t. ii. p. 470.

† Vide Leuret, “Anat. Comparée du Système Nerv.” tome i. 1839, p. 402, and a fuller account in Gratiolet’s edition of the same work, tome ii. 1857, p. 74.

‡ P. A. Fish, “The Brain in the Fur-Seal, *Callorhinus ursinus*; with a Comparative Description of those of *Zalophus*, *Phoca*, *Ursus*, and *Monachus*,” Journal of Comparative Neurology, vol. viii. nos. 1 and 2, July 1898, p. 79.

“The conditions . . . might naturally suggest homology with the ape and human calcar and that the splenial fissure, in this seal possessing a postcornu, might be homologized with the occipital [the context shows that this term undoubtedly refers to the parieto-occipital sulcus] or calcarine fissure in Man.”



developmental history, which thoroughly establishes the homology. In some of the larger Ungulata, for example *Camelus*, there is a small posterior cornu into which the "splenial" eminence projects just as the calcar bulges into the Primate ventricle. In the Cetacea the splenial sulcus is obviously identical with that of the Carnivora and Ungulata, and its resemblance to the calcarine sulcus of the Primates is enhanced in some genera, e. g. *Hyperoodon*, by its relation to a distinct posterior cornu of the ventricle, which has been described by Ziehen \*.

During my investigations on the brain in the Edentata, the results of which were presented to this Society almost four years ago, I was very much astonished to find a well-defined swelling on the mesial wall of the lateral ventricle of *Orycteropus* which simulated the calcar avis. My astonishment was due to the fact that at that time I was not acquainted with any of the above-mentioned writings and knew only of the teaching of such anatomists as Flower, Turner, and Cunningham, who have so formally and categorically denied the possibility of homologizing the calcarine sulcus of the Primates with the splenial furrow in other mammals. Nevertheless the mass of evidence in favour of the identity of these two furrows, which a study of the Edentata and other mammals yielded, seemed to me to be so overwhelming, that I adopted this view even though it is in direct contradiction to the views of those anatomists, from whom I have acquired much of my knowledge of the mammalian brain †.

Among the heterogeneous collection of Edentata, there are found all stages in the form of the calcarine sulcus intermediate between the Carnivore condition on the one hand, and the simpler form found in the Chiroptera, Marsupialia, and Insectivora (*i. e.* if *Galeopithecus* can be called an Insectivore). In no true Insectivores is there a calcarine, or "splenial" (as most anatomists would call it) sulcus. But this is not necessarily of any great significance, because in the smaller Chiroptera and (Polyprotodont) Marsupials there is no such sulcus, although the larger members of these Orders (*Pteropus*, *Cynonycteris*, *Thylacinus*, and practically all the Diprotodontia) present a typical one.

The most peculiar fact, so far as the distribution of this furrow is concerned, is its absence in most of the Rodentia. In only one or two of the largest members of the Orders, such as *Hydrochærus*, is any such furrow developed; and even in these few cases it is small and insignificant. In the Monotremata the calcarine sulcus cannot be recognized; moreover, it is highly probable that none of the mesial sulci in the hemisphere of *Echidna* represents the calcarine sulcus of the Metatheria and Eutheria.

The most primitive form of the calcarine sulcus is seen to best advantage in such brains as those of *Thylacinus*, *Trichosurus*, *Phascogale*, *Macropus*, *Cynonycteris*, *Pteropus*, and most of the Edentata. Of these I select for representation the hemisphere of *Pteropus poliocephalus*, not that it differs in any respect from any of the other forms enumerated, but because the presence of the calcarine sulcus in this genus has

\* W. Kükenhal and Th. Ziehen, "Ueber das Centralnervensystem der Cetaceen, nebst Untersuchungen über die vergleichende Anatomie der Placentaler," Denkschriften der medicin.-naturwissensch. Gesellschaft zu Jena, 1893, pp. 89, 117, *inter alia*.

† Trans. Linn. Soc. ser. 2, Zool. vii. 1899, pp. 328-333.

been categorically denied by Ziehen\*. He states that in the brain of *Pteropus medius* (which is identical with that of *P. poliocephalus*†) none of the sulci which he labels  $\pi$ ,  $\sigma$ , and  $\rho$  in the Lemurs (corresponding respectively to the paracalcarine, calcarine, and retrocalcarine of my account) are present; but he believes the sulcus  $\alpha$  (the intercalary of these notes) to be prolonged backward around the splenium. It is quite unnecessary (because the discrepancy is so obvious) to point out how little accord there is between this view and that held by the same writer with regard to the Carnivora and Cetacea.

The comparison of the section through the hemisphere of *Pteropus* (fig. 54) with that of *Lemur* and *Canis* is quite sufficient to show the identity of the conditions in the three forms.

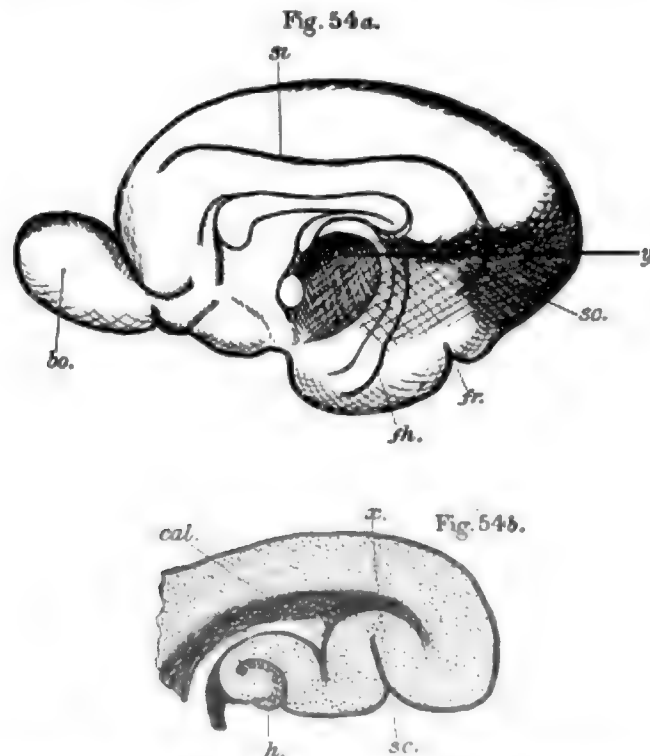


Fig. 54 a.—*Pteropus poliocephalus*. Mesial aspect of the right cerebral hemisphere.  $\times 3$ .

Fig. 54 b.—*Pteropus poliocephalus*. A horizontal section through the posterior part of the hemisphere in the plane y (fig. 54 a).

In order that the relationship of the calcarine sulcus to the retrocalcarine and paracalcarine sulci may be rightly appreciated and its systematic value may be correctly appraised, it is necessary to consider certain other aspects of this problem.

The exaggerated importance which Owen‡ had attached to the calcar avis or so-called

\* Arch. f. Psychiat. 1896.

† Vide Gustav Retzius, "Zur Morphologie der Fascia Dentata," &c., Biolog. Unters. N. F. viii. 3, Taf. 14. fig. 3.

‡ Proc. Linn. Soc. 1858; also Annals & Mag. Nat. Hist., June 1851, Rede Lecture, and elsewhere.

"hippocampus minor," as a supposed distinctive feature of the human brain, led to a very heated controversy in 1861, during the course of which many anatomists subjected the "occipital" region of the brain in the Primates to a careful examination. One of the most valuable results of this unseemly strife was the introduction of the useful term "calcarine sulcus," which Huxley conferred upon the external furrow, the obverse of which forms the calcar avis in the lateral ventricle. Another result was the demonstration by Huxley, Flower, and others, that the calcar and its sulcus are not distinctive of the human brain, but are common to all the Apes or even Primates, according to Flower\*.

The calcar was first described early in the eighteenth century by Morand†, who likened the little projection on the mesial wall of the posterior cornu of the lateral ventricle (in the human brain) to a cock's spur and called it "*ergot*," the Latin equivalent of which is "*calcar avis*." Towards the latter part of the same century Vicq-d'Azyr‡ called it "*hippocampus minor*," because it appeared to be continuous with the larger swelling known as *hippocampus [major]*.

According to Broca, Cruveilhier § was probably the first writer to definitely refer to the constancy of the sulcus which produces the calcar, or "*anfractuosité de la cavité digitale*" as he called it.

In 1854 Gratiolet wrongly believed ¶ that the sulcus in question was continued into the hippocampal fissure, and included both under the latter name. This misconception helped to establish the misleading name "*hippocampus minor*" which Vicq-d'Azyr had introduced. The merit belongs to Huxley of pointing out the fallacy of which these names were the expression, and, by reinstating the name calcar avis and introducing the new term "calcarine sulcus," he rid Descriptive Anatomy of a serious source of confusion. I have introduced these historical notes here, because it has unfortunately become necessary to emphasize once more, firstly, the contention of Huxley that the term "*hippocampus minor*" should be for ever banished with the misconception which it symbolizes; and that the term "*calcar avis*," or simply "*calcar*," be substituted; and, secondly, that the true and exact significance of the term "*sulcus calcarinus*" may not be forgotten, as it is by most modern writers on the anatomy of the brain. As the name "*calcarine*" is derived from "*calcar*," it necessarily follows, as Huxley showed, that *the essential part of the sulcus and that strictly deserving the title "calcarine" is the furrow which produces the calcar avis*. But Huxley himself pointed out that the sulcus "extends beyond the calcar and the posterior cornu"¶. And he also did much more than this. For, profiting by the earlier and not wholly successful attempt of Gratiolet, he for the first time clearly distinguished among the complex arrangement of mesial sulci the distinct hippocampal, calcarine, collateral, and parieto-occipital elements. Huxley

\* "On the Posterior Lobes of the Cerebrum of the Quadrumana," Phil. Trans. 1862, pp. 185 *et seq.*

† Morand, 'Histoire de l'Académie,' 1744.

‡ Vicq-d'Azyr, 'Traité d'Anatomie et de Physiologie,' tome i. 1786.

§ Cruveilhier, 'Anatomie Descriptive,' 1<sup>ère</sup> Edition, 1836, tom. iv. p. 663.

Modern neurological literature contains innumerable repetitions of this error.

¶ "The Brain of *Atelæ*," Proc. Zool. Soc. 1861, p. 255.

thus clearly anticipated most of the recent work in this region, by distinguishing the parieto-occipital from the calcarine sulcus and by recognizing that the latter extends backward, far beyond the calcar.

Within recent years Cunningham\* has called attention to a differentiation of the calcarine sulcus into anterior and posterior elements, which are to be distinguished the one from the other not only by a difference in the time and mode of development, but also, in many cases, by their features in the adult human brain. The "anterior calcarine" sulcus is the first to develop and becomes an extremely deep sulcus, which is wholly responsible for the bulging of the calcar in the ventricle. In other words, it is the true "calcarine sulcus."

The sulcus which Cunningham calls "posterior calcarine" develops later and quite independently of the anterior sulcus; it never becomes as deep as the former; as a rule it does not share in the formation of the calcar, and in many cases it is separated from the anterior or calcarine sulcus by a submerged fold of cortex. It is, to use Cunningham's own words, "a *secondary sulcus* in every sense of the term"†. It is therefore of a very different nature to the true calcarine sulcus, and, as it is convenient to have a distinctive name, I shall call it "retrocalcarine," because it is placed on the caudal side of the calcar.

In his great monograph on the human brain, Retzius‡ objects to Cunningham's teaching and says that he "does not believe that such a fundamental difference between the fore and hinder parts of the fissure, as Cunningham sees, can be recognized. The front part grows at least as often without a hinder addition and itself forms the hinder part." The close of this quotation is interesting, as being practically a concession of the writer's position and also by reason of its bearing upon the condition found in the Apes, which Cunningham regards (erroneously, I believe) as differing essentially from that found in the human brain. For a study of Comparative Anatomy makes it abundantly clear that in the case of two sulci developing in the same line, it often happens that the minor sulcus seems to be formed merely by a prolongation of the major sulcus rather than as an independent element. The posterior part was called "calcarine" only because it was supposed to be part of the true calcarine sulcus; but as this is not strictly so, the distinct name "retrocalcarine" has been introduced. This has been done, not for pedantic reasons, but because a separate name becomes absolutely necessary in Comparative Anatomy, where the fundamental distinction between the two elements becomes more pronounced.

Describing the development of the sulci in a Sheep's brain, Krueg says that, in a foetus 19 cm. long, two furrows have appeared: one on the lateral aspect is the faintly marked representative of the fossa Sylvii of the human foetus, and the other is a more definitely

\* D. J. Cunningham, "Contributions to the Surface Anatomy of the Cerebral Hemispheres," Mem. Roy. Irish Academy, July 1892.

† *Op. cit.* p. 49.

‡ 'Das Menschenhirn,' Jena, 1896.

The passage here quoted is taken from an article by Cunningham, *Journal of Anatomy and Physiology*, vol. xxxi. p. 595. See also Retzius, 'Biologischen Untersuchungen.'

marked sulcus on the mesial surface, which he calls "*splénialis*"\*, a name which has been very generally adopted. He adds:—"According to Ecker† the fissura parieto-occipitalis‡ develops in the human brain at about the same time as or soon after the fissura Sylvii: I am very much disposed to consider it as the homologue of my fissura splénialis" (p. 309). In a later memoir he describes the splénial sulcus in Unguiculate Mammals. He explains the peculiarities of the fissura hippocampi and the fissura rhinalis as lines of demarcation between cortical areas which are histologically different. Both of these fissures develop very early, and after their appearance there is a long pause before any other sulcus presents itself. The first one to do so in the Cat's hemisphere is the sulcus splénialis (in a foetus of 10+4.5 cm. long). In such a foetus it appears "as a flattened arc surrounding the posterior end of the corpus callosum and the upper end of the hippocampal fissure, midway between these structures and the upper and hinder margins of the hemisphere" §.

From a comparison of these interesting facts with those brought to light by Cunningham and Retzius, the conclusion is forced upon us that, if any sulcus on the mesial surface of the human hemisphere is to be regarded as the homologue of the "splénial" sulcus of the Sheep and Cat, it must be, not the morphologically unstable and unimportant parieto-occipital sulcus which Krueg suggests, but the true "calcarine sulcus."

That such an interpretation was not entertained by Krueg is obvious from his quotation of Meynert's happy guess ||, when he called "a short ascending branch of the f. splénialis" in the Bear together with a short accessory furrow under it the "sulcus occipitalis," and the f. splénialis itself the "sulcus calcarinus" ¶. On the same page Krueg quotes Benedikt as calling "the f. splénialis in the Bear the fissura occipitalis inferior . . . and the mesial part of the f. medilateralis the fissura calcarina" (p. 642)\*\*.

If, however, we adopt Krueg's idea, we must, in the light of our fuller knowledge of the developmental history of the human brain, regard the splénial sulcus as partly homologous to the calcarine.

In Broca's Collected Works (p. 321, fig. 26) a short oblique furrow is represented in the hemisphere of a Roebuck, which obviously corresponds to the sulcus Krueg calls "postsplénialis." Broca calls this sulcus "the analogue of the calcarine fissure," whereas he regards the splénial sulcus as part of the "limbic fissure." He

\* Julius Krueg, "Ueber die Furchung der Grosshirnrinde der Ungulaten," Zeitsch. f. wissensch. Zool. Bd. xxxi. p. 308, November 1878.

† A. Ecker, "Zur Entwickl. der Furchen und Windungen der Grosshirnhemisph. im Fötus des Menschen," Arch. f. Anthropol. iii. Bd., 1865.

‡ Ecker is wrong in this; for it is the calcarine, and not the parieto-occipital, sulcus which develops first.

§ Julius Krueg, "Ueber die Furchung der Grosshirnrinde der zonoplacentalen Säugetiere," Zeitschr. f. wissensch. Zool. Bd. xxxiii., 1880.

|| Meynert, 'Archiv f. Psychiatrie,' Bd. vii., 1877. The context shows that Meynert's suggested homologies were little else than sheer guesswork.

¶ Krueg, *op. cit.* p. 641.

\*\* Benedikt, 'Anatomische Studien an Verbrechergehirnen,' Wien, 1879.

adds in explanation that he "calls it *sillon calcarin*, although the *ergot* (calcar) from which its name is derived exists only in the Primates" (p. 322). It is clear from this that Broca believes that the postsplenic sulcus represents that sulcus of the Primate brain which produces the calcar, *i. e.* the true calcarine and not the retrocalcarine sulcus.

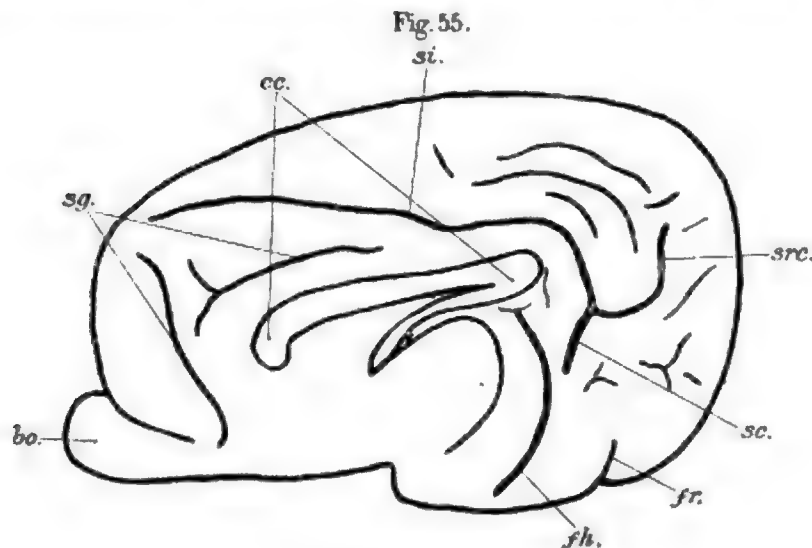
In the brains of most Carnivora and Ungulata, as well as in many other mammals, a series of inconstant and exceedingly variable sulci make their appearance behind the calcarine (*i. e.* the retrosplenic part of the splenic) sulcus. In the smaller members this so-called "postsplenic" sulcus tends to run parallel to the "splenic" sulcus. But in the larger Carnivores, especially the Bears and Seals, and the larger Ungulates, such as the Cow, Horse, and Camel, there are usually a series of postsplenic sulci; and it usually happens that the deepest of these pursues a course which is not parallel to the calcarine (splenic), but inclines obliquely upward and backward at an angle with the latter. It not unfrequently happens that this "retrocalcarine" sulcus, as we may not inaptly term it, joins the calcarine. The tendency of the retrocalcarine element to pursue a course which is not parallel to the calcarine becomes more pronounced in such mammals (the Seals, for example) as possess a distinct caudal (or occipital) prolongation of the hemisphere. It is, therefore, not surprising to find that in those mammals—viz., the Primates—in which such a caudal extension of the hemisphere is most pronounced (so that the mechanical factors which tend to induce the cortex to become folded in the longitudinal direction are most potent), the retrocalcarine sulcus always assumes the longitudinal, and never the vertical, direction\*. It is still further determined in this course by the increasing obliquity of the calcarine sulcus, which is brought about partly by the backward extension of the hemisphere itself, and partly by the caudal elongation of the corpus callosum. In fact, the direction of the calcarine and retrocalcarine sulci is brought, as the result of the operation of these various factors, so accurately into the same line that in most Primates the less important retrocalcarine element seems to develop merely as a caudal prolongation of the more precocious and stable calcarine sulcus.

The brain of the Camel affords a striking illustration of these facts. The mesial surface of its cerebral hemisphere exhibits a triradiate group of deep sulci behind the splenium of the corpus callosum (fig. 55). Superficially these furrows appear to be joined to one another; but if their lips be separated, it will be found in some cases that the deep calcarine sulcus is confluent with neither the intercalary sulcus, as in most mammals, nor with the retrocalcarine sulcus, as in most Primates, but is separated from both by deeply submerged gyri, as is frequently the case in the human brain. It is, moreover, noteworthy that the bulging (calcar) which is pushed into the definite posterior cornu of the ventricle in this brain is produced wholly by the calcarine, and not by the retrocalcarine nor intercalary sulci.

\* The variability of this sulcus clearly shows that it possesses little stability, and cannot be regarded as a definitely fixed landmark like the true calcarine. It probably arises in order to relieve the tension of the expanding "visual" cortex, and its form and position are determined by conditions which are chiefly, if not wholly, mechanical. In these respects it presents a most marked contrast to the calcarine sulcus.



It is obvious, therefore, that it is the retrocalcarine and not the true calcarine sulcus which Broca has called "sillon calcarin" in the brains of the Roebuck and Ass. The



*Camelus dromedarius.*

Mesial aspect of the right cerebral hemisphere. Nat. size.

true calcarine sulcus in these mammals is represented in a part of the great furrow which he calls "limbic."

If my view of this matter be correct, most recent English writers have departed much further from the true interpretation than even Krueg and Broca.

In his well-known memoir "On the Convolution of the Brain," Sir William Turner \* gave expression to very decided opinions concerning the calcarine sulcus and posterior cornu. Writing about the brain of *Hapale jacchus*, he states:—"There is no splenial fissure, but opposite the splenium a distinct calcarine fissure" (p. 141). This amounts to a categorical denial of the homology of the calcarine and splenial sulci.

On the same page he makes the further statement (in this case referring to the brain of *Nycticebus* [*Stenops*]) that "the calcarine fissure . . . proves the presence of both posterior cornu and calcar avis" †. The data upon which this statement is based are borrowed from Flower (Phil. Trans. 1862), who says, in the memoir quoted, that he found it impossible to determine in this particular brain "whether or not the posterior cornu exists." Nevertheless Turner goes on to say that "if the surface of the hemisphere be examined with the view of determining the presence of an occipital lobe by the evidence of a fissure, the calcarine fissure is that which is to be regarded as of primary importance" (p. 141). This means presumably that there is no "occipital lobe" in any mammals other than the Primates, seeing that the "calcarine fissure" is supposed to be absent. The splenial sulcus, which occupies the position of the calcarine sulcus, is regarded by Turner as merely a part of the calloso-marginal sulcus (p. 144).

\* Journ. Anat. and Phys. vol. xxv. 1890.

† I have shown in these notes that there is no posterior cornu in the brain of *Nycticebus*.



Alongside these remarkable statements we might place Flower's comment concerning "the absence of anything resembling the calcarine fissure [in the Cat's brain]" (Trans. Zool. Soc. vol. v. p. 109). Flower's failure to recognize the identity of the calcarine and splenial sulci is perhaps the more unintelligible, because he admits (*vide supra*) that a patent posterior cornu is not a condition absolutely necessary for the existence of a calcar and a calcarine sulcus.

In his earlier work on the Seal's brain \*, Sir W. Turner suggests homology between the collateral sulcus of the Primates and splenial sulcus of "Quadrupeds"; and, if I read aright the memoir quoted above (Journ. Anat. and Phys. vol. xxv.), the splenial sulcus may be represented in the Primates by both the calloso-marginal and collateral sulci. In comparison with the calcarine, these two furrows (calloso-marginal and collateral) are of very minor importance †.

Many other writers might be quoted to show the conflicting views which are put forward to explain the morphology of the splenial sulcus on the one hand and the calloso-marginal, calcarine, and collateral on the other. It will, however, suffice for our purpose if we consider chiefly the views of two modern writers, whose views are diametrically opposed, the one to the other. Professor Ziehen finds in the Primate brain some representative of almost every sulcus of the common mammalian brains; whereas Professor Cunningham adopts the extremist view expressed in his statement that, "except in the case of certain of the main furrows (*e. g.* Sylvian ‡, hippocampal), it is very questionable indeed if there is any homological correspondence between the sulci of a primate brain and the sulci of a quadrupedal brain." These remarks, written several years ago, have been confirmed as recently as this year, at the meeting of the British Association.

Ziehen has discussed the representation of the calcarine sulcus among the general body of mammals in several of his memoirs; but we shall chiefly consider the remarks in his memoir on the Prosimian brain § as being most pertinent to this discussion. In his description of the "calcarine group" of furrows in *Nycticebus*, he says that the *retro-calcarine* sulcus (which he labels *c*) is undoubtedly the *calcarine* fissure; and the calcarine

\* 'Challenger' Reports.

† Concerning the latter sulcus Alex. Hill gives utterance to a characteristic remark:—"There is no doubt in my mind as to the homology of the octorhinal [rhinal] fissure of the Dog with the collateral fissure in Man. . . . To use any other term than collateral fissure appears to me pedantic" ("The Hippocampus," Phil. Trans. 1893, p. 408). As the rhinal fissure is one of the few furrows which can certainly be recognized by the histological features of its lips, we can with certainty state, even if we are thereby stigmatized as pedantic by Dr. Hill, that the rhinal fissure is *not* the collateral sulcus.

(One is surprised to find so cautious a writer as Professor D. J. Cunningham apparently subscribing to the same view; for he makes the statement that the "*incisura temporalis* [*i. e.*, a remnant of the rhinal fissure] . . . may be regarded as a forward prolongation of the collateral fissure" ('Manual of Practical Anatomy,' vol. ii. 1896, p. 501). This error is probably to be explained by the fact that the part of the rhinal fissure which is on the caudal side of the *incisura temporalis* is commonly regarded by Human Anatomists (who disregard the distinction between the pyriform lobe and the neopallium in the so-called uncinat gyrus) as part of the collateral sulcus.

‡ The case of the Sylvian is rather unfortunate, as will be seen later, for the sulcus called "Sylvian" in the "Quadrupeds" is *certainly not* the homologue of the Primate "Sylvian fissure."

§ Archiv f. Psychiat. Bd. xxviii. 1896, p. 903.

(his  $\rho$ ) is the continuation of the retrocalcarine and not of the paracalcarine (his  $\pi$ ). The furrow  $\pi$  merely cuts into the upper lip of  $\rho + \sigma$ . In reference to this statement, he calls attention to Bischoff's memoir \*. In his discussion of the homologies of the calcarine group of sulci, Ziehen compares the furrows of the Prosimian brain with those of the Carnivora, and especially *Phoca hispida*. Like Broca, he regards the posterior branch of the splenial sulcus ("ramus horizontalis posterior") as the calcarine sulcus, and the "occipito-temporal part of the splenial" as the "stem of the f. parieto-occipitalis and fissura calcarina" (p. 919). The confusion in these statements arises from the failure to recognize that it is the so-called "stem of the parieto-occipital and calcarine furrows" which alone deserves the title "calcarine" †, whereas the furrow he calls "calcarine" is really the retrocalcarine. But if the calcarine sulcus of the Prosimiæ is represented by the end piece of the splenial sulcus in the Carnivora, why does he consider the obvious homologue of the latter in *Pteropus* to be the sulcus  $\alpha$  (calloso-marginal or intercalary), and not the sulcus  $\rho$  (calcarine) ?

A similar confusion of the true calcarine sulcus and the posterior calcarine has been made by the German Anatomical Nomenclature Commission, calling the former "f. occipito-calcarina" and the latter "f. calcarina," in spite of the fact that Huxley introduced the name "calcarine" to distinguish that sulcus which produces the calcar, i. e. the so-called "occipito-calcarine." Burt Wilder, who has disagreed with the conclusions of the German Committee on so many other points, seems to embody the same confusing use of terms in his system of nomenclature.

Many other writers, such as Benedikt and Meynert, apply the term calcarine to that portion of the sulcus which can only by courtesy, as it were, be so called, because it is really a separate sulcus, the retrocalcarine, which has secondarily become confluent with the true calcarine. If it were not for this confusion of terms, the conclusions at which these writers have arrived might have been received as an approximately accurate expression of the homologies existing between the furrows of the Carnivora and the Primates; but this can hardly be said of them in their present confusing form ‡. Pansch's criticism of the teaching of Meynert is utterly futile in the light of our present knowledge. The climax of his argument—"Wo ist bei einem Raubthier ein Calcar avis?"—becomes meaningless, if we compare figs. 51 and 53 of this work §.

The works of the English anatomists Turner and Cunningham are in direct conflict with all the other writings quoted above. I have already referred to Turner's views.

\* Sitzb. d. bayer. Akad. d. Wissensch. 1870, p. 478.

† I. e., if the slightest attention be paid to the definition given by Huxley when he coined the word calcarine. The calcarine sulcus is the furrow which produces the calcar.

‡ Theodor Meynert, "Die Windungen der convexen Oberfläche des Vorder-Hirnes bei Menschen, Affen und Raubthieren," Arch. f. Psychiatrie, 1877.

Maurice Benedikt, "Nouvelle contribution à l'Anatomie comparée du Cerveau," Bull. de la Soc. d'Anthrop. de Paris, 4<sup>e</sup> série, t. vii. March 1896, p. 226.

§ Adolf Pansch, "Bemerkungen über die Faltungen des Grosshirns und ihre Beschreibung," Arch. f. Psychiat. Bd. viii. 1878, p. 238.

Cunningham has said that "we are not in a position at present to offer an opinion . . . upon the statement that the calcarine fissure is also developed in brains below the Primates" \*. Five years later he stated that, "except in the case of certain of the main furrows (*c. g.* Sylvian, hippocampal), it is very questionable indeed if there is any homological correspondence between the sulci of a primate brain and the sulci of a quadrupedal brain." In spite of all the research in this field since these quoted passages were written, Cunningham has recently reaffirmed his unaltered belief in his view in these words:—"We now know that the primate cerebrum was not only distinguished from that of all lower mammals by the possession of a distinct occipital lobe, but also by having imprinted on its surface a convolutionary design which, in all but a few fundamental details, was different from that of any other order of mammals" †.

What is this occipital lobe, which is so distinctive of the Primates? Cunningham himself does not tell us what he means by the expression. If it is merely the caudal prolongation of the hemisphere above the cerebellum, then many large Carnivores have an equal or perhaps better right to be regarded as Primates than some of the Lemurs; and if it is the posterior cornu which is the diagnostic sign, then the Lemurs cannot be regarded as Primates, whereas the Seals, the Camel, and some Cetacea are to be classed along with the Apes. If, however, it is the calcarine sulcus which, to quote Turner, "determines the presence of an occipital lobe," how can we draw a line of demarcation in respect to this feature between the Primates and other mammals? So far as I am aware, these are the only possible criteria of an "occipital lobe," and none of them, either separately or in conjunction, can be regarded as exclusively distinctive of the Primates.

If we refuse to admit the homology of the calcarine sulcus of the Primates and the retrosplenial part of the splenial sulcus of other mammals, we have a far more difficult problem to solve. For an explanation is then needed of the reasons for regarding as different two sulci (in different groups of mammals) presenting identical relations to the lateral ventricle and to the neighbouring brain-regions, a similarly precocious appearance in ontogeny, and a constancy under varying conditions in mammals which have widely diverged from the primitive stock. Why should we suppose that the splenial sulcus, which is the most constant and most precocious neopallial furrow in the mesial wall of the hemisphere in the Marsupialia, Chiroptera, Edentata, Carnivora, Ungulata, and Cetacea, fails to develop in the Primates, and that another and a different furrow develops in the Primates *in a position which exactly corresponds* to that occupied by the splenial in other mammals and *at the same epoch* in development? Such a phenomenon is utterly inconceivable. The calcarine and the retrosplenial part of the splenial sulci are certainly identical.

But, it may be argued, the calcarine sulcus is an independent furrow, whereas the "splenial" is prolonged into a supracallosal course—the intercalary sulcus. But in the Myrmecophagidæ, Bradypodidæ, and Manidæ the calcarine is not joined to the inter-

\* "Complete Fissures of the Human Cerebrum," *Journal of Anatomy and Physiology*, vol. xxiv. p. 343.

† Presidential Address, Section II, Anthropology, British Association, September 1901.

calary sulcus, and in some of the smaller Marsupials, such as *Trichosurus*, there is no intercalary sulcus, the simple calcarine furrow alone being present.

It may further be objected that a true calcarine sulcus can exist only when there is a posterior cornu of the lateral ventricle. If so, the Lemurs cannot have a calcarine sulcus, whereas the Seals and the Camel possess such a furrow.

It is quite impossible to frame any definition of a calcarine sulcus or of an "occipital lobe" which can be raised as a barrier between the Primates and the other mammals, such as Cunningham would have us erect. The calcarine sulcus and the calcar avis are not the exclusive property of the Primates, but are the common heritage of all the Metatheria and Eutheria.

In most mammals this sulcus becomes joined to the intercalary, a furrow of little morphological importance; but in the Primates the backward prolongation of the corpus callosum so alters the direction of the calcarine that it forms an acute angle with the line of the intercalary, so that for purely mechanical reasons the two furrows fail to unite, and the calcarine becomes confluent with the retrocalcarine, which is another furrow of quite secondary importance.

It is not without considerable significance that these phenomena occur in an equally pronounced form in the Lemurs as in the Apes, in spite of the fact that the mechanical conditions favouring such a sundering of the calcarine-intercalary junction are at least equally marked in many Carnivores, in which the separation does not occur. It would, however, be unwise to attach too great an importance to this fact, because we find the calcarine sulcus separated from the intercalary in the Anteaters, Sloths, and Pangolins.

The fact that no trace of the parieto-occipital sulcus is found in the Hapalidæ and several of the smaller Cebidæ seemed to suggest the possibility of that furrow being a purely Simian feature, which had become evolved in the Apes only. I was therefore inclined at first to follow Flower's teaching, and regard the paracalcarine sulcus of the Lemurs as one of the limbs of the bifid extremity of the retrocalcarine sulcus of the Apes. But the fact that it branches off from the point of union of the calcarine and retrocalcarine sulci shows that it occupies a position analogous to that of the lower extremity of the parieto-occipital sulcus in the higher Apes.

But are we justified in calling this furrow parieto-occipital? Most writers do so without the slightest hesitation.

In order to settle this point I have examined the brain in every genus of Monkeys, and have found that in the higher Apes, where the true parieto-occipital sulcus of Human Anatomy can alone be said to exist, this furrow is composed of two and frequently more elements. In the majority of cases, however, there are two sulci, dorsal and ventral, which overlap to a considerable extent, the intervening area of cortex usually becoming submerged so as to obscure the dual nature of the resultant furrow. The ventral furrow I have called "paracalcarine," because it pursues a course alongside the calcarine sulcus in its most typical form, *e. g.* in *Simia*. The dorsal sulcus is obviously due to the bias which is given to the developing cortex near the dorsal edge by the intraparietal sulcus. This furrow becomes so sharply bent that it forms an acute

angle, which points toward the mesial surface, and so affects the neighbouring area that a vertical sulcus usually develops in response to this mechanical bias.

The paracalcarine sulcus in the Lemurs obviously represents the ventral element only, and not the whole of the parieto-occipital.

I have introduced the term "intercalary" to distinguish a furrow which has hitherto received no exclusive title. In most mammals it is joined to the calcarine, and the complex is called "splenial": in the Primates it is separated from the calcarine and joined to the genual sulcus to form the calloso-marginal sulcus. In many Carnivores it is also joined to the crucial sulcus. It is therefore intercalated between the three furrows—calcarine, genual, and crucial—to any or all of which it may be joined. In spite of its constancy in the Mammalia, the intercalary furrow is morphologically unstable and readily becomes broken up into several fragments in the larger Ungulates and Carnivores. A careful examination of the behaviour of this furrow in the whole Mammalia leads me to regard the paracalcarine as being equivalent to the separated posterior fragment of the intercalary sulcus, or as a new compensatory-calcarine furrow developed only in the Primates. In the case of sulci which possess so little individuality and morphological value as the intercalary and the parieto-occipital, it is of little use attempting to establish any exact correspondence, because this can hardly be said to exist even in two hemispheres of the same brain. All that can be said with certainty is that the tension of the growing cortex, which would be relieved in the Carnivora by the confluence of the intercalary and calcarine sulci, is instrumental in forming the paracalcarine sulcus in the Lemurs. This does not, however, imply the identity of the two furrows. The instability of the paracalcarine element is shown in the Cebidæ: in *Callithrix* it is either absent or very diminutive, in *Chrysotrrix* it forms the typically vertical ventral element of the parieto-occipital sulcus, and in *Nyctipithecus* it is horizontal. Of course the latter cannot be described as homologous with the typical furrow of *Chrysotrrix*, but merely as the expression of the same causal factors. There can therefore be no strict homology between such an unstable furrow and any sulcus, and especially such a variable element as the intercalary, in other mammals.

When we consider how fickle this sulcus is, the fact of its extreme constancy of form and relations in all the Lemurs, not excepting even the aberrant *Tursius* and *Chiromys*, becomes a valuable testimony to the closeness of the bond of affinity which unites all the Prosimiæ. In fact, a study of the mesial aspect of the hemisphere affords convincing proof of this undoubted kinship.

In many Lemurs of various genera an oblique sulcus (*b*) appears on the ventral side of the retrocalcarine sulcus. A comparison of this with a series of Primate brains shows it to be the posterior part of that composite and morphologically unimportant furrow which is called "collateral" in the brain of Man and the Apes.



THE MORPHOLOGY OF THE SULCI ON THE LATERAL AND DORSAL  
ASPECTS OF THE CEREBRAL HEMISPHERE.

Innumerable attempts have been made, with results as varied as they are numerous, to solve the problem of determining to how great an extent, if at all, it is possible to institute exact comparisons between the sulci of two brains.

If the two hemispheres of any highly convoluted brain be compared, a certain number of furrows will be found in each, which cannot be exactly homologized with any sulcus in the other hemisphere. And not unnaturally the number of such "incomparable" elements increases when we compare the hemispheres of different individuals, species, genera, families, and orders. The crucial question is thus reduced to the enquiry as to the possibility of recognizing any sulci as the common property of several Orders.

The most divergent and mutually contradictory views are held at the present time on this subject. Thus there is the negative teaching, which is perhaps most forcibly and dogmatically expressed in a posthumous memoir by A. J. Parker in these words:—"The mistake is often made . . . of attempting to compare their [the Mammalia in general] convolutional characters with those of the Primates, including Man . . . We cannot expect, nor do we find, any exact homological relations between the convolutions of this phylum [sic] and those of other mammalian phylla [sic]"\*. The same view is expressed in a less pronounced form by D. J. Cunningham.

The view of Gegenbaur may be summed up in his own words by the statement "dass eine Homologie nur in sehr engen Grenzen besteht und bei sehr vielen gar nicht durchführbar ist" (Vergl. Anat. der Wirbelthiere, i. Band, 1898, p. 769).

Although in many of his earlier memoirs Turner had instituted comparisons between the sulci in different mammalian Orders, yet in his latest contribution he comes to the conclusion that in each Order of Mammals a special pattern of sulci is evolved peculiar to itself.

Most other writers who have in any way dealt with this subject have come to the conclusion that it is possible to homologize the sulci of Primates to a greater or less extent with those of other mammalian Orders, but there is an infinite variety of suggestions as to the exact manner in which this is to be done.

Before we consider a few of the suggested interpretations, it will conduce to clearness if I first explain, by a reference to the Cat's brain, the nomenclature employed in describing the sulci in Orders other than the Primates.

The furrow commonly called "Sylvian fissure" is an offshoot of the rhinal fissure: as the usual designation is undoubtedly erroneous, I shall call it the pseudosylvian sulcus (fig. 56 *b*). The sulcus which is best known by the name "presylvian" (*Owen*), I have termed "orbital" for reasons which will be apparent later. The furrow which is commonly called "posterior suprasylvian" has been designated by its original name "postsylvian" (*Owen*), not only because the latter is more appropriate, but chiefly that

\* "Morphology of the Cerebral Convolutions with Special Reference to the Order of Primates," *Journal of the Acad. of Natural Science*, Philadelphia, 2nd series, vol. x. 1896, p. 276.

the name "suprasylvian" may be reserved for the other sulcus, of such vastly greater importance, to which it often happens to be linked in the Carnivora.

The other names are sufficiently explained by the accompanying diagrams (figs. 56 *a* and *b*). One of the earliest attempts to compare this pattern of sulci—which we may

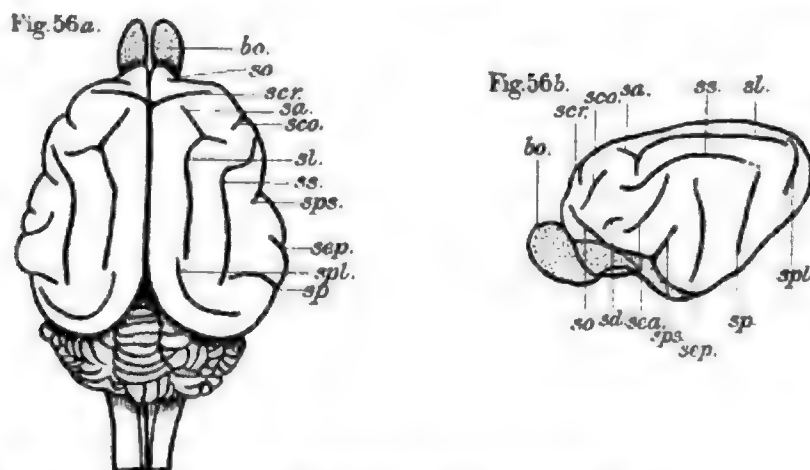


Fig. 56 *a*.—*Felis domestica*. Dorsal aspect of brain. Nat. size.

Fig. 56 *b*.—*Felis domestica*. Lateral aspect of the left cerebral hemisphere. Nat. size.

regard as the common Mammalian plan—with the sulci of Man and the Apes was that of Pansch \*. He regarded the upper of the three curved sulci on the lateral aspect of the Dog's brain (*i. e.*, presumably the conjoint lateral and coronal sulci) as the boundary of the postcentral convolution (*i. e.*, presumably the intraparietal sulcus of Turner, the "interparietal" sulcus of most Continental writers). The middle and lower curved sulci (*i. e.*, the suprasylvian, postsylvian, and ectosylvian) are not represented, according to this writer, in the brain of the Primates.

In Owen's 'Anatomy of Vertebrates,' 1868, the orbital (presylvian) sulcus is regarded as part of the Sylvian fissure.

Hitzig, as the result of a physiological investigation into the distribution of the motor areas in the Dog and Ape, came to the conclusion that the central sulcus of the latter is represented in the former by the ansate and the anterior part of the suprasylvian sulci †.

In another memoir by Pansch the orbital sulcus of the Carnivora is regarded as the representative of the precentral sulcus of Apes: the suprasylvian [in his former paper it was the corono-lateral] corresponds to the intraparietal, and the coronal sulcus to the central (Rolando's) ‡.

Meynert, who committed the extraordinary error of thinking the crucial sulcus [which

\* "Ueber d. typische Anordnung d. Furchen u. Windungen auf den Grosshirnhemisphären der Menschen u. der Affen," Arch. f. Anthropologie, Bd. iii. p. 227 (1868).

† 'Untersuchungen über das Gehirn.' Leipzig, 1874.

‡ "Ueber gleichwerthige Regionen am Grosshirn der Carnivoren und der Primaten," Centralb. f. d. med. Wissensch. no. 31, p. 641 (1875).



he called central, *i. e.* Rolando's] absent in the Bear, considers that the central sulcus of Man is represented in the Carnivora by the coronal sulcus \*.

Broca regarded the orbital (presylvian) sulcus of Carnivora as the representative of the human sulcus of Rolando †.

In 1878 Pansch once more returned to the discussion of this problem, which he had been considering for more than ten years. After criticising the views of other writers, and more especially Meynert's, he maintains ‡ the same views concerning the homologies of the coronal and suprasylvian sulci which he advanced three years before (*op. cit. supra*).

On physiological grounds Munk regards the crucial sulcus of Carnivores as the homologue of the central sulcus of Primates, and cites the recent work of Kükenthal and Ziehen and of Eberstaller in support of this view. This enumeration of the different views which have been enunciated by different writers might be considerably extended if it would serve any useful purpose §.

It will be noticed that all of these writers (as well as those who arrive at negative results) attempt to institute direct comparisons between highly specialized representatives of the Carnivora like the Dog and Cat and the higher Apes. No writer has taken the obvious precaution of testing the accuracy of his suggestions by an appeal to the simplest and most generalized types in the two Orders: nor, again, is it altogether clear why the vast majority of writers invariably seek for homologues for the sulci of the Primates in only one Order of Mammals (in most cases the Carnivora), unless it be because the non-Primate type of sulci is seen in its most specialized form in these latter.

Every writer (including even those who, like Parker and Cunningham, deny the homologies of the sulci in the Primates and other Orders) commits the fundamental error of regarding the so-called Sylvian fissure of the Carnivora and other Mammals as the representative of the Sylvian fissure of the Primates. But there cannot be the slightest doubt that the two furrows are not homologous.

The only means of arriving at any reliable conclusions as to the possibility of homologizing the sulci of the Lemurs with other mammals is to critically study the behaviour of these furrows in the Mammalia as a whole. And as this is the only means of truly appreciating the relationship of the Prosimian brain to that of other mammals, I propose to briefly summarize here the data relating to the cerebral sulci in other Orders which have been stated more fully elsewhere ||.

First of all, the behaviour of those sulci which I have represented in the Cat's brain may be studied in the Carnivora. In the Primates, the two most stable furrows of the neopallium, and those to make their appearance earliest in development, are the calcarine

\* "Die Windungen der convexen Oberfläche des Vorder-Hirns bei Menschen, Affen und Raubthieren," Arch. f. Psychiatrie, Bd. vii. p. 256 (1877).

† "Anatomie comparée des circonvolutions cérébrales," Rev. d'Anthropologie, 1878.

‡ "Bemerkungen über die Faltungen des Grosshirns und ihre Beschreibung," Arch. f. Psychiatrie, Bd. viii. 1878.

§ Brief reviews of the Literature will be found in memoirs by J. N. Langley ("The Structure of the Dog's Brain," Journal of Physiology, vol. iv. pp. 268-276); Jules Soury ("Système Nerveux Central," tome ii., especially pp. 910 & 915); and Flatau and Jacobsen ("Vergl. Anatomie," *op. cit.*)

|| Catalogue of the Royal College of Surgeons, Second Edition, vol. ii. 1902.

sulcus on the mesial surface (with which at present we are not concerned) and the Sylvian fissure on the outer surface. It might reasonably be assumed therefore that, if the sulcus usually called "Sylvian fissure" in the Carnivora were correctly so-called, it would be the most constant and most precocious furrow on the outer aspect of the neopallium. But this is not so. For if the developmental history of the neopallial sulci be studied in any Carnivore \*, it will be found that several sulci, such as the suprasylvian and coronal, make their appearance long before the pseudosylvian sulcus. Then, again, if the brain be studied in the whole assemblage of Carnivores, it will be found that the suprasylvian, coronal, and lateral sulci exhibit far greater stability and maintain their characteristic features with far greater constancy than does the pseudosylvian sulcus. And in the more generalized and primitive Viverridæ the latter becomes very imperfect and inconstant, and even at times disappears entirely. Occasionally the same phenomenon occurs in some of the other Carnivores: I have seen the pseudosylvian sulcus of the Cat reduced to very diminutive proportions, and the ectosylvian sulci deepened to compensate. It is clear, therefore, that the so-called "Sylvian fissure" of the Carnivora is not the morphologically stable and precocious furrow which we should expect if it were the true representative of the similarly-named feature of the brain in the Primates. Moreover, the nature of this false Sylvian furrow varies considerably within the limits of the Carnivora. In the *Æluroidea*, as for example in the Cat's brain, the lips of the pseudosylvian sulcus are formed by the first arcuate gyrus of Leuret, *i. e.* the strip of neopallium which is bounded peripherally by the ectosylvian sulci. In the *Arctoidea* (as was long ago demonstrated by Sir William Turner, and recently confirmed by Holl and the writer [Catalogue of Royal College of Surgeons †]), the whole of the first arcuate gyrus is buried in the false Sylvian furrow, so that the lips of the latter are formed not by the *first* (as in the *Æluroidea*) but by the *second* arcuate gyrus of Leuret, *i. e.* by the area bounded peripherally by the suprasylvian and postsylvian furrows. And in the *Pinnipedia* (as I have recently shown in the above-quoted Catalogue, p. 296) the whole of the anterior limb of the second arcuate gyrus tends to become buried in the great cleft-like so-called "Sylvian fissure," so that in many Seals the anterior lip of the furrow is formed by the *third* arcuate gyrus of Leuret. And if a series of Carnivores be examined, all intermediate stages will be found between these extreme types.

Moreover, it has been shown by Holl ‡, who has so admirably demonstrated the real nature of the so-called "Sylvian fissure" in Carnivores and Ungulates, that the claustrum also extends beyond the area depressed in the pseudosylvian sulcus, even in the *Arctoidea*; so that, if anyone is inclined to attach importance to this structure as an indication of the extent of the insula (or area submerged in the Sylvian fissure), it is obvious that the pseudosylvian sulcus of Carnivores is in no sense homologous with the true Sylvian fissure of the Primates.

By far the most precocious and most stable sulcus on the lateral aspect of the neopallium in the Carnivora is the suprasylvian (*i. e.*, the furrow which most writers

\* I have examined embryonic brains of the Cat, Dog, and Bear, and have confirmed the teaching of Krueg (Zeitsch. f. wissensch. Zool. Bd. xxiii.) in this matter.

† Vol. ii. (2nd ed. 1902) p. 277, fig. 154.

‡ Arch. f. Anat. u. Phys., Anat. Abth. 1899 and 1900.

call "suprasylvian anterior"). Its caudal extremity may or may not be joined to the relatively unimportant postsylvian sulcus (*i. e.*, the "suprasylvian posterior" auct.); the latter is not only much more variable, but develops much later than the true suprasylvian sulcus. In most Carnivores the two sulci are united to form a regular arc around the pseudosylvian sulcus. But it often happens in almost every genus, and constantly in *Herpestes* and its allies, as well as in many Seals, that the suprasylvian is not joined to the postsylvian sulcus. The morphological value and importance of the two furrows is so vastly different, that I have thought it advisable to wholly discard the common and misleading title "suprasylvian posterior," and return to the original name "postsylvian" (Owen), which is both simpler and more accurate, as the further discussion will show.

The ectosylvian sulci are features of little morphological importance, and are to be regarded as furrows compensatory to the pseudosylvian sulcus. In many genera both ectosylvian sulci are absent: in the Hyenidae the anterior ectosylvian sulcus is absent; and in the Bears the two sulci are submerged. Even when present the sulci are exceedingly variable.

Next in importance to the suprasylvian sulcus come the orbital (presylvian), coronal, and lateral, and, after a wide interval, the crucial, postlateral, arcuate, and prorean sulci in that order.

The presylvian (or, as I prefer to call it, "orbital") sulcus makes its appearance at a very early period, and is almost as constant as the suprasylvian. It usually becomes considerably prolonged so as to join the rhinal fissure below and so as to extend near to the dorso-mesial edge of the hemisphere above. But both these phenomena must be regarded as secondary modifications, which take place under the influence of purely mechanical factors, and are therefore devoid of great morphological importance. The true fundamental orbital element is a small furrow placed in the neopallium alongside the anterior end of the rhinal fissure: as such it is perhaps the most constant and one of the most stable of all the neopallial sulci in the Mammalia. The coronal and lateral sulci are second in importance only to the suprasylvian and orbital. The former is perhaps very slightly the more precocious, but occasionally this sulcus is absent when the lateral sulcus is present, as sometimes happens in *Herpestes*. [This is also especially the case in Rodents and in many Marsupials. On the other hand, the coronal sulcus is often present when the lateral sulcus is absent in some Ungulates, and especially in *Procavia*.] In the Carnivora as a whole these two sulci are very constant, and in most cases they are united to form one furrow.

The direction of the coronal sulcus is subject to considerable variation in the different families. In the larger members, and especially the Ursidae, it becomes almost transverse; whereas in the simple, generalized Viverridae its direction is almost sagittal.

A postlateral sulcus is often united to the caudal end of the lateral, but it is exceedingly variable and may be entirely absent. In its simplest form it often consists of a small transverse furrow behind (and not joined to) the lateral sulcus.

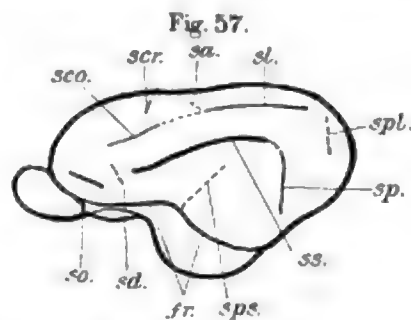
The crucial sulcus, which is often regarded as a distinctively Carnivore feature, is not constant. Its size is exceedingly variable. So large does it become in the Bear that

Meynert refused to regard it as the "crucial" sulcus, and called it "central." In the Viverridæ it is often absent, and its simplest form is exhibited in some of the members of this family as a small depression on the dorsal surface of the hemisphere, a short distance in front of the outwardly-bent anterior end of the lateral sulcus.

The ansate sulcus is a branch of the lateral, which develops behind the crucial sulcus. It is not constant, and when present is subject to great variation.

Much less constant than any of these furrows is the sulcus which Krueg calls "diagonalis." It is often present in the Felidæ as a separate element: more often its identity is lost by merging into the anterior ectosylvian sulcus or the suprasylvian.

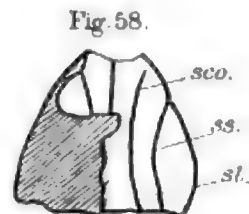
If we represent graphically the inferences drawn from the foregoing discussion as to the features of the primitive Carnivore, a scheme such as the accompanying diagram (fig. 57) would be the result. This is practically the brain of *Viverra*.



A scheme representing the sulci in a hypothetical generalized Carnivore.

That this is really the primitive Carnivore type will be shown by an examination of the brain-casts of the Eocene Carnivora.

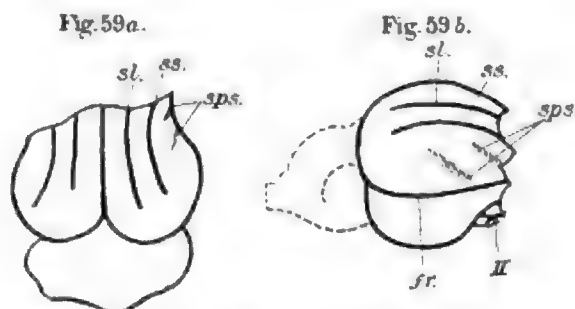
Thus in a natural cast of the brain of *Stenoplesictis Cayluxi* in the British Museum (M. 1723) there is a conjoint corono-lateral sulcus (which is quite sagittal in direction) and a well-defined suprasylvian sulcus, as in *Viverra*. There is no sign of crucial, pseudosylvian, or postsylvian sulci.



*Stenoplesictis Cayluxi*. Dorsal aspect of a natural cast of the cranial cavity. Nat. size.

In the excellent natural cast of the cranial cavity of *Cynohyaenodon Cayluxi* (British Museum, M. 4499)—another Carnivore, which, like *Stenoplesictis*, comes from the Upper Eocene formations of France—we find similar lateral and suprasylvian sulci, and two very shallow furrows representing the pseudosylvian sulci [a similar phenomenon is often

found in the Viverrida]. There are neither postsylvian nor postlateral sulci; but the suprasylvian and lateral sulci extend almost to the posterior extremity of the hemisphere\*.



Figs. 59 a & b.—*Cynohyrcodon Cayluri*. (a) dorsal and (b) lateral aspects of a natural cast of part of the cranial cavity. Nat. size.

If we turn to the examination of the lateral surface of the hemisphere in the Ungulata (leaving out of account certain sulci, such as the intercalary, which often leaves the mesial and extends on to the dorsal surface†) we shall find in *Procarvia*, which is perhaps the most generalized member of the Order, an arrangement of sulci which is obviously identical with that of the hypothetical primitive Carnivore.

The suprasylvian and coronal sulci closely resemble those of *Viverra*, and especially the Eocene Carnivores, both in position and extent. The lateral sulcus is usually less well-developed, and is always separated from the coronal sulcus; but there cannot be the slightest doubt as to its identity with the similarly-named sulcus in the Carnivora. In some cases the lateral sulcus is absent.

The pseudosylvian sulcus is almost always absent, but in one brain (of eight examined) I found a furrow resembling that sometimes seen in *Viverra*. That this sulcus was no mere vascular furrow was shown by the presence of a vertical postsylvian sulcus‡ in that brain and not in others. Another instance of a similar phenomenon is shown in Turner's figure of the brain of *Hyrax* [*Procarvia*] (Journ. Anat. and Physiology, vol. xxv. 1900).

A small typical orbital sulcus is almost invariably present, although it has been overlooked by both Krueg and Turner. There is no diagonal sulcus.

If the developmental history of the cerebral hemispheres be studied in a series of Ungulates §, it will be found that the earliest sulci to make their appearance on the outer surface of the hemisphere are those which from their relations and behaviour are

\* There is not much resemblance between this cast and that figured by Filhol. There is no doubt, however, that, even if this is not what it is represented to be, it is certainly an Eocene Carnivore.

† As a similar phenomenon is presented in the brains of certain Carnivores, such as *Helictis*, and, less decidedly in *Meles*, there can be no doubt as to the homologies.

‡ This showed that there was a furrow of sufficient depth to lend a bias to the neighbouring cortex.

§ Such investigations have been made by Krueg (Zeitsch. f. wissenschaft. Zoologie, Bd. xxxi.), and more recently by Paul Martin ("Zur Entwicklung der Gehirnfurchen bei Katze und Rind," Arch. für wissenschaft. u. prakt. Thierheilk., Bd. xxi. Heft i., 1895), and I have studied this problem in embryos of *Chis*, *Bos*, *Capra*, *Sus*, and *Camelus*.

Bradley has published a few data concerning the Horse's brain in the Journ. Anat. and Phys. vol. xxxiii. pp. 215 & 587.

obviously the suprasylvian, orbital, and coronal sulci. In their subsequent development all of these sulci differ very considerably from their homologues in the Carnivora, so that it is important to bear in mind that these sulci are regarded as homologous not only because they are the most constant and similarly-placed furrows, but because their mode of development demonstrates their identity in the two Orders.

Holl has recently demonstrated that the sulcus commonly called "Sylvian fissure" in the Ungulata is not homologous with any one of the various types of pseudosylvian sulcus found in the Carnivora. The "Carnivore pseudosylvian" sulcus is sometimes found in the Ungulata, *e. g.* in the genus *Bos*, but it is not that which is commonly called "Sylvian fissure." The latter (which we may call the "Ungulate pseudosylvian" sulcus) is formed by the meeting of two sulci, which are analogous to the ectosylvian sulci of the Carnivora\*.

After the sulci mentioned above, the most constant furrows are the lateral and diagonal sulci. The former sulcus is not linked to the coronal sulcus as so often happens in the Carnivora; but it is sometimes joined to the suprasylvian sulcus. The diagonal sulcus is much more constant than it is in the Carnivora, and it is almost always placed just in front of the anterior end of the suprasylvian sulcus.

It is doubtful whether true homologues of the postsylvian and postlateral sulci are ever found in the Ungulata.

If we review the whole Ungulate Order so as to determine the constant sulci, it will be found that those furrows only will be picked out which, as the evidence of embryology shows, represent those also found in the hypothetical primitive Carnivore.

If we next examine the Edentata the same fundamental plan of sulci is again found.

Thus in the genus *Bradypus* we find pseudosylvian, suprasylvian, lateral, coronal, orbital, and diagonal sulci arranged in a manner so like that seen in *Felis*, that one cannot question the homologies implied in the nomenclature just used. The developmental notes published by Pouchet show that one is thoroughly justified in maintaining this view. In the nearly allied, but larger, genus *Choloepus* the pseudosylvian sulcus disappears; it thus adds further testimony to the slight importance of this sulcus.

In the Anteater (*Tamandua*) there is always a definite orbital sulcus and a conjoint coronal-lateral, but it is a peculiar fact that in some cases the suprasylvian sulcus may be absent, although in others it is well-developed. There is no pseudosylvian nor diagonal sulcus.

One of the most interesting and instructive brains in the whole mammalian series is that of *Myrmecophaga jubata*; and all the more so because it is subject to peculiar variations.

The normal or common type of brain exhibits a conjoint coronal-lateral, a postlateral, a postsylvian, an orbital, and a prorean sulcus, as in the Carnivora, and in addition a pseudosylvian sulcus of a peculiar nature. Moreover there are sometimes shallow

\* Holl, "Ueber die Insel des Ungulatengehirnes," Arch. f. Anat. u. Phys. 1900. Compare also Catalogue of the Royal College of Surgeons, 2nd Edition, vol. ii. figs. 194 (p. 339) and 197 (p. 343).



depressions representing diagonal\*, posterior ectosylvian, and crucial sulci of the Carnivore-type.

The feature of most interest, however, is the pseudosylvian sulcus. This usually consists of a shallow depression above the bend of the rhinal fissure: there is a well-defined posterior lip, but no anterior lip. From the apex of the depression a deep and well-defined sulcus begins and arches backward close to the upper end of the postsylvian sulcus.

The reader will observe that so far no mention has been made of the suprasylvian sulcus, the most stable sulcus on the outer surface of the hemisphere in the Carnivora and Ungulata. It might, perhaps, be supposed that, as this sulcus is sometimes absent in *Tamandua*, it might also be absent, as a rule, in *Myrmecophaga*. But it is hardly likely that a cerebral hemisphere which is provided with lateral, coronal, orbital, post-lateral, postsylvian, pseudosylvian, prorean, and even diagonal, posterior ectosylvian and crucial sulci, should lack just that particular sulcus which is the most constant and stable sulcus in the Mammalia. Such a phenomenon is so highly improbable as to be almost inconceivable. There can be no doubt whatever that the suprasylvian sulcus is present as the deeply-incised, dorsal, arcuate appendage of the pseudosylvian sulcus.

Fortunately there is an anomalous brain in the Collection of the Royal College of Surgeons [D. 281, Catalogue, p. 223, fig. 95] which proves that this is so. On the left hemisphere of this brain the condition described above is found; whereas on the right hemisphere the suprasylvian sulcus† is separated from the pseudosylvian sulcus and joined to the postsylvian, as in most Carnivores.

In *Orycteropus* the suprasylvian sulcus is only poorly developed, whereas the coronal, lateral, orbital, and prorean sulci are exceedingly well-developed. There is no trace of a pseudosylvian sulcus.

In *Manis* there are typical suprasylvian, orbital, corono-lateral, and pseudosylvian sulci, as in *Bradypus*.

In the Armadillos the orbital sulcus is always, and the suprasylvian sometimes present.

In many of the Rodents there is an extraordinary paucity or even absence of sulci. The lateral is perhaps the most constant sulcus, and the orbital and coronal sulci are found in many Rodents. In *Hydrochærus* and *Lagostomus* there is a suprasylvian sulcus; and in the former numerous other furrows of doubtful homology. The most interesting brain among the Rodentia is that of *Dolichotis*. In addition to the typical orbital and sagittally-directed corono-lateral sulcus there is a suprasylvian sulcus like that of *Lagostomus*, but it is joined to a pseudosylvian sulcus to form a conjoint Sylvian furrow, such as is usually found in the Edentate *Myrmecophaga*. These forms are of particular interest in comparison with the condition found in the Lemurs, as will be apparent later‡.

\* The diagonal sulcus, both of the Bradypodidae and the Myrmecophagidae, is always directed upward and forward as in the Ungulata and Primates, and is not subject to the irregularity and changes in direction which we find in the Carnivora.

† A comparison of the two hemispheres shows that the suprasylvian sulcus is certainly present in both.

‡ See Catalogue of the Royal College of Surgeons, 2nd Edition, vol. ii. p. 205, fig. 75.



In the Chiroptera the suprasylvian and lateral sulci are *sometimes* present in the genera *Pteropus* and *Cynonycteris*, and resemble the corresponding furrows in the Edentate *Tamandua*.

In the true Insectivora there is usually an *orbital* sulcus only. This is particularly well-developed in *Gymnura*. The little brain of the aberrant *Galeopithecus* is peculiarly rich in sulci. It possesses a very deep and unusually extensive suprasylvian sulcus of unusual form, and in addition well-defined orbital and pseudosylvian sulci.

The smaller Polyprotodont Marsupials resemble the Insectivora in possessing no well-defined sulcus except the orbital on the outer surface of the cerebral hemisphere. In *Thylacinus* and most of the Diprotodontia there are also suprasylvian, pseudosylvian, and prorean sulci; and in *Phascotomys* and many of the Macropodidæ there is a typical lateral sulcus\*.

If all of these scattered data be collated it will be possible to determine those features which are the common property of all the Metatheria and of those Eutheria which do not belong to the Order Primates. If we attempt to form a hypothetical type of cerebral hemisphere embodying all these features, it must be macrosomatic and must present a well-defined rhinal fissure. It must have a deep and well-defined suprasylvian sulcus, a small orbital sulcus which neither joins the rhinal fissure nor is prolonged far in the mesial projection: coronal and lateral sulci which are nearer the sagittal than the transverse direction and which are quite separate. In addition there *MAY* be pseudosylvian, postsylvian, postlateral, oblique, ansate, and crucial sulci, for none of these are the exclusive property of one Order, but all, as the brief review given above shows, tend to appear in all mammals. Moreover, there is to be noted a tendency in several Orders (in *Myrmecophaga* among the Edentates, in *Dolichotis* among the Rodents, and in the Seals among Carnivora) for the area which separates the overlapping parts of the suprasylvian and pseudosylvian sulci to become submerged or so reduced that the two furrows form one sulcal complex (fig. 60).

If, after this review of the conditions which prevail among the Mammalia in general, the plan formed by the sulci in the Lemurs be examined, it will be apparent that the arrangement in the latter is unquestionably a slightly modified form of the hypothetical common mammalian type. This exact reproduction of just those sulci which are most stable in other mammals, and the variability shown by just those furrows which are less stable in other mammals, can be no mere fortuitous phenomena, but positive evidence of morphological identity.

There can be no doubt that the Sylvian fissure of the Lemurs is formed by the peculiar union of the suprasylvian sulcus with the less stable pseudosylvian of other mammals. Just as the suprasylvian element in this complex is the only sulcus of the lateral surface which is absolutely constant in all Lemurs, so it is the most stable sulcus in the Mammalia generally. That it is really the suprasylvian sulcus which is found in the Lemurs is abundantly shown by the peculiar condition found in *Chiromys*.

In order of constancy the orbital, lateral, and coronal sulci come next, just as also

\* These homologies in the Marsupialia are suggested by a comparison of the mode of development of the furrows in the brain of *Macropus* and that exhibited in other mammals, especially certain Ungulata.

happens in the Mammalia as a whole. Next in order follows the postsylvian sulcus, again as in other mammals. And finally, the most variable Prosimian features—the postlateral, diagonal, and crucial furrows—are exactly those which come next in the order of frequency among mammals in general.

The homologies thus suggested are so revolutionary and so opposed to all the current teaching, that it is necessary to submit each sulcus seriatim to the closest scrutiny in the light of all the comparative evidence available, either in the facts of direct observation or in the writings of other anatomists. At the same time, it will be convenient to extend the range of comparative studies and include the Apes and Man.

#### THE MORPHOLOGY OF THE SYLVIAN FISSURE.

The Sylvian fissure is found in its complete and typical form only in the human brain. The peripheral lips of three sulci become opercular and approach until they meet: the peculiar pattern thus formed upon the surface by the meeting of these labia is commonly called the Sylvian fissure.

The region which becomes overlapped by the opercula is called the insula Reilii and is bounded by three sulci—the inferior, superior, and anterior limiting sulci. If the human brain be compared with a sufficiently complete series of brains of Primates, it will become so obvious as to amount to an absolute demonstration that the inferior (morphologically posterior) limiting sulcus represents the pseudosylvian, the superior limiting sulcus the suprasylvian, and the anterior limiting sulcus the diagonal sulcus, respectively, of the Lemurs and other mammals.

It has been clearly shown by Marchand\* and Cunningham† that the anterior limiting sulcus of the island of Reil is the homologue of the fronto-orbital sulcus of the Anthropoid Apes. If anyone is disposed to dispute this contention and follow the lead of Hervé, Eberstaller, Waldeyer, and Giacomini (among others), a glance at the series of brains of Anthropoid Apes, and especially those of the Gorilla, in the Museum of the Royal College of Surgeons will convince him of his error‡. The anterior limiting sulcus of the insula is certainly the homologue of the fronto-orbital sulcus of the Apes. The latter is best developed in the genera *Anthropopithecus*, *Simia*, and *Hyllobates*, but is constantly found in a less well-developed condition in *Semuopithecus*, *Papio*, and frequently in other genera of Old-World Apes and sometimes also in the larger members of the family Cebidæ.

In the Hapalidæ and the smaller Cebidæ, and sometimes also in the smaller Cercopithecidæ, this sulcus is absent. It is therefore interesting to note its presence in many individuals of the genus *Lemur* as well as in some of the Indrisinæ. Undue importance must not, however, be attached to this fact, because the fronto-orbital sulcus of the Lemurs and Apes is almost certainly the homologue of the diagonal sulcus of the Carnivora, Ungulata, and Edentata.

\* "Die Morphologie des Stirnlappens und der Insel der Anthropomorphen," Jena, 1893, pp. 91 *et seq.* (Arbeiten aus d. patholog. Inst. zu Marburg, Bd. ii.).

† "The Insular District in the Cerebrum of the Anthropoid Apes," Journ. of Anat. and Phys. vol. xxxi. pp. 1 *et seq.*

‡ See especially specimen D. 658, Coll. Surg. Catalogue, p. 439.

The only writer who has attempted to seek for the common mammalian homologue of this fronto-orbital sulcus of the Lemurs is Ziehen \*. He came to the conclusion that it represented the presylvian (orbital) sulcus of other mammals; but the fallacy of his argument is quite patent and capable of easy refutation. Ziehen regards the sulcus which I have called "orbital" in the Lemurs as the representative of the "intraorbital" sulcus of the Carnivora, and the diagonal (fronto-orbital) sulcus as the presylvian (which I call orbital). Thus he attempts to homologize a sulcus which is one of the most stable features of the Prosimian brain with an unimportant furrow like the intraorbital which is found in only a few of the larger Carnivora and is morphologically of no importance; and, on the other hand, he suggests the identity of the exceedingly stable presylvian (orbital) sulcus of the Carnivora with the fronto-orbital sulcus which is found only in the genera *Lemur*, *Propithecus*, and *Indris* of all the Prosimiæ, and not constantly even in these. He attempts to justify this by the statement that the presylvian sulcus may be absent in a Carnivore, and quotes the example of *Herpestes*. I have, however, examined ten cerebral hemispheres of *Herpestes*, and have never found the orbital (presylvian) sulcus absent, though it is always very small †. But even if it were always absent not only in one but in several genera of Carnivora, this would not justify the homology of one of the most constant sulci of this Order with perhaps the most unstable sulcus in Lemurs.

In the literature of cerebral morphology the orbital (presylvian) sulcus of the Carnivora has been represented as the homologue of many sulci by different writers. According to Owen, Meynert, and many others (even in Edinger's recent text-book, 1899), it represents part of the Sylvian fissure; according to Pansch it is the precentral sulcus; and according to Broca and Eberstaller (and also Soury in his great work 'Le Système Nerveux Central,' 1899) it is the homologue of the central (Rolando's) sulcus.

The evidence of Comparative Anatomy (and by this I do not mean the futile attempt to compare the brain of *one* specialized Carnivore like the Cat with that of the highest Primate) shows decisively that the presylvian sulcus of the Mammalia cannot possibly be represented in the Primates by any of these four sulci—Sylvian (Owen), precentral (Pansch), central (Broca), or fronto-orbital (Ziehen). The orbital (presylvian) sulcus is perhaps the most constant sulcus (in the neopallium) in the Mammalia. It is found in the brain of almost every Carnivore †, Ungulate, Cetacean, Edentate (excepting *Chlamydophorus*), and in all Rodents, Insectivores, and Marsupials which have any cerebral sulci. It is therefore highly improbable that such a stable sulcus should either be entirely absent or be represented by an inconstant element in the Primates. Moreover, the brain of the Primates possesses a sulcus in the same position in the hemisphere as the presylvian occupies in other mammals; and this sulcus is the most constant furrow in front of the Sylvian fissure. This can be no other than the orbital sulcus (the "triradiate" sulcus of Turner; the "presylvian" sulcus of Owen). The correctness of this identity of presylvian and orbital sulci becomes more conclusively demonstrated as the range of comparison increases. If we compare, for example, the presylvian sulcus of the Rodent *Dolichotis*,

\* Arch. f. Psych. Bd. xxviii.

† It is actually absent in the Herpestine *Crossarchus*.

or of the Carnivore *Viverra* or the Ungulate *Procavia*, with the orbital sulcus of such a Prosimian brain as that of *Galago* or even *Lemur*, one cannot deny that the two sulci are morphologically identical. If we examine a large series of human brains, it will be found that the stable portion of the orbital sulcus consists of a deep oblique sulcus, the posterior end of which approaches close to and often joins the outer limb of bifurcation of the olfactory sulcus, just as the presylvian sulcus of the Carnivore's joins the rhinal fissure; but the simple linear form of the orbital sulcus of Man is usually disguised by a series of inconstant branches, so that it seems to lose the simplicity of form it possesses in most Apes. If this fundamental part of the human orbital sulcus be compared with the presylvian sulcus of the larger members of the other Mammalian Orders, such, for example, as the Camel and the Seals, a demonstration of the identity of these two furrows will be afforded which is quite as striking as the similarity of the presylvian sulcus of *Dolichotis* to the orbital of *Galago*. Such instances might be multiplied without limit.

So that, if we take into consideration all the facts which a study of the brain in *all* mammals yields, there is a mass of evidence amounting to absolute demonstration that the sulcus variously called presylvian, supraorbital, orbital, and triradiate in different mammals is fundamentally one and the same furrow.

Between the orbital sulcus and the lower end of the Sylvian fissure we occasionally find a furrow in the Lemurs and the New-World Apes, and generally in the Old-World Apes: this is the fronto-orbital sulcus. With regard to this homology in the Lemurs, I quite agree with Ziehen. But, on the other hand, the evidence which I have been able to collect points conclusively to the truth of the suggestion of Eberstaller and Cunningham, that the fronto-orbital sulcus of the Apes [and Lemurs] is the anterior limiting sulcus of the insula of the human brain.

In most Ungulates, in many Carnivores, and in the Bradypodidæ and *Myrmecophaga*, a small oblique sulcus makes its appearance in the position exactly corresponding to that occupied by the fronto-orbital sulcus in the Primates: it is called the diagonal sulcus (Krueg), and is placed between the orbital and the suprasylvian sulci. It is highly improbable that a small oblique sulcus such as the diagonal (especially in the Ungulates and in *Bradypus*) should develop in the analogous position in three different Orders so as to exactly reproduce the features of the fronto-orbital sulcus of the Lemurs and Apes without being homologous. The probability that "diagonal," "fronto-orbital," and "anterior limiting" are merely different names for the corresponding furrows in different mammals is immeasurably greater than the reverse.

The evidence upon which Professor D. J. Cunningham chiefly relied to clinch the proof of the identity of the fronto-orbital and anterior limiting sulci, was the distribution of the claustrum. This consists of the deeper part of the cortex which composes the island of Reil. In the human brain the claustrum becomes separated from the rest of the cortex by a definite medullary layer in a region coextensive with the insula, *i. e.* so far forward as the anterior limiting sulcus. In the Chimpanzee [and the same holds also for the Orang and Gorilla] the claustrum extends as far forward as the fronto-orbital sulcus. In the Cercopithecidæ and Cebidæ it is unfortunately the fact that we cannot use such evidence with the same degree of definiteness, because the anterior extremity of the

claustrum becomes so diffuse that its extent cannot be accurately mapped out. But its distribution shows clearly that the anterior part of the insula is freely exposed on the surface of the brain, as it is in the Anthropoid Apes. In the genus *Lemur* the claustrum is an exceedingly plump and well-defined structure. It extends backward as far as the posterior [inferior] limiting sulcus (which is the pseudosylvian sulcus), and extends forward slightly beyond the fronto-orbital (diagonal) sulcus (fig. 60 *a*), at the same time becoming somewhat diffuse.

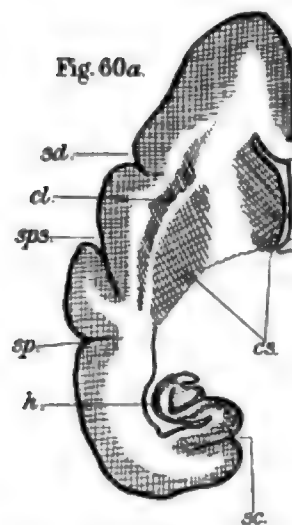
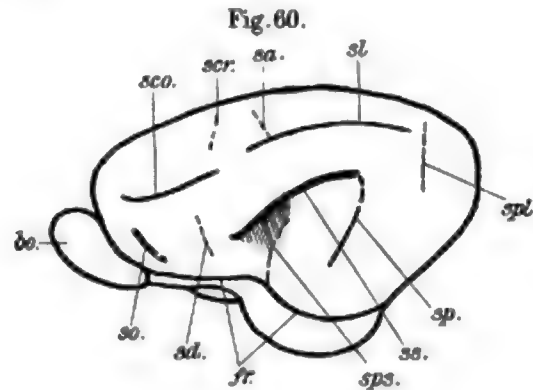


Fig. 60.—A scheme representing the sulci common to most Mammalia.

Fig. 60a.—*Lemur fulvus*. Horizontal section through the brain.  $\times 2$ .

This may perhaps seem to throw doubt upon the homology of this sulcus in the Lemurs and the Anthropoid Apes. It is impossible to appreciate the true value of such evidence until we know more than we do at present of the significance of the claustrum\*.

\* This subject has been studied by T. E. Clark ("Comparative Anatomy of the Insula," Journ. Comp. Neurology, vol. vi, June 1896, pp. 59-101, 35 figures), and more recently by M. Holl ("Ueber die Insel des Carnivorengehirns," Arch. f. Anat. u. Physiol. [Anat. Abth.] 3 u. 4, pp. 217 *et seq.*, 1899; "Ueber die Insel des Ungulatenghirns," *ibidem*, 5 u. 6, pp. 295 *et seq.*, 1900).

Among Clark's conclusions it is stated that "the claustrum may include parts of areas other than the insula" (p. 91), *i. e.* it may extend beyond the situations of the limiting sulci.

The most revolutionary and novel suggestion in the foregoing discussion is the homology of the suprasylvian sulcus of mammals in general partly with the superior limiting sulcus and partly with the upper (or posterior) part of the Sylvian fissure of the Lemurs and Apes.

Such an interpretation of the morphology of the cerebral sulci has never been suggested hitherto; and yet I believe that, if the identity of these two sulci be denied, it is impossible to homologize the majority of the sulci in the brain of the Primates with those of other mammals. For if the furrow which is deepest, most stable, and most precocious in the Carnivora, Ungulata, and Edentata is not represented in the Primates, and, moreover, by that particular sulcus which is also most constant and develops earliest, then it is utterly futile to seek for the homologues of the other more variable sulci.

The only writer (Ziehen) who has seriously attempted to homologize the Prosimian sulci with those of other mammals [or, more strictly, with those of the Carnivora], found representatives in the Primate brain for the lateral, coronal, ansate, crucial, presylvian, ectolateral, medilateral, intraorbital, and postsylvian [his "fissura suprasylvia posterior"] of the Carnivora, and yet imagined that the most stable and deepest sulcus of the Carnivora—the suprasylvian sulcus\*—was missing when so many unimportant sulci are reproduced. Such a suggestion is utterly inconceivable; and, even if we knew nothing of the instructive phenomena exhibited in *Chiromys*, in *Myrmecophaga*, and in *Dolichotis*, the conclusion must be forced upon us that either the suprasylvian sulcus is merged in the Sylvian complex, or it is impossible to institute exact comparisons between the sulci of the Primates and any other mammals.

It is quite unnecessary to point out the fallacy of the old teaching of Pansch and Meynert, that the suprasylvian sulcus represents the intraparietal sulcus of the Primates.

Several writers have appreciated the obstruction in the way of a satisfactory interpretation of this region; but I believe no one has hitherto suggested the solution which all impartial observers must admit to be true.

Thirty years ago Gervais saw the difficulty, when he wrote:—"Lemurs never have more than two convolutions around the Sylvian fissure, whilst even the smallest Carnivores have three"†; but did not explain which of the Carnivore furrows disguised its identity by merging in another sulcus.

Quite recently Holl recognized that the "Sylvian fissure" of *Lemur* is composed of two separate sulci; but he suggested the ectosylvian, and not the suprasylvian, as the dorsal element‡.

\* Ziehen (Arch. f. Psych. Bd. xxviii.) says:—"Der vordere Bogenschnitt der F. suprasylvia (*i. e.* the true sulcus suprasylvius) fehlt dem Halbaffengehirn" (p. 921).

† Journ. de Zoologie, tome i. p. 27.

‡ Arch. f. Anat. u. Phys., Anat. Abth. 1900.



In the interpretation of the morphology of sulci, one is not disposed to place any great reliance upon physiological evidence; for, even supposing that the functions of the various regions were known, it does not necessarily follow that homologous areas are homodynamic in different Orders. Nevertheless it is of interest to note how fully the results of physiological research support the view that the upper part of the Sylvian fissure represents the suprasylvian sulcus.

Thus Ferrier records \* that stimulation of the dorsal lip of the suprasylvian sulcus in the Cat causes retraction of the angle of the mouth and movement of the eyes to the opposite side, whereas pricking or sudden retraction of the opposite ear is the result of applying the electrodes to the lower lip of the suprasylvian sulcus. *Stimulation of the corresponding lips of the upper part of the Sylvian fissure in a monkey (Macacus) produced the same results as that elicited by excitation of the lips of the suprasylvian sulcus in the Cat (fig. 335).* The results obtained by Ferrier in the case of *Lepus* (p. 734) are in full accord.

In Edinger's summary of the results of physiological experiment on the cerebral cortex he represents two diagrams †, borrowed from Gustav Mann, showing the lateral aspect of the brains of the Cat and Rabbit respectively: in these the suprasylvian sulcus is represented separating two areas labelled respectively "Oculomotor" [the dorsal] and "Auris" [the ventral]. Edinger inserts a diagram of the human brain alongside these, and labels the dorsal lip of the posterior end of the Sylvian fissure "Oculomot." and the ventral lip "Auditus."

Now, as it would be absurd to imagine that the results adopted by Ferrier, Schäfer, Mann, and Edinger were in any way biassed by such a (to them) rank heresy as the belief in the identity of the Sylvian and suprasylvian sulci, the evidence which they unconsciously produce is of value as an indication that one who entertains such a belief cannot be accused of flagrantly disregarding physiological data. Moreover, this wholly unexpected support from the physiologists is the last link in a long chain of irrefutable evidence (only a few links of which have been incorporated in these notes) that the upper [caudal] part of the Sylvian fissure of the Primates and the dorsal limiting sulcus of Reil (the "opercular" sulcus of Marchand) represent the suprasylvian sulcus of quadrupeds.

The stable suprasylvian sulcus, by its "union" with that variable suprarhinal kink which I have called "pseudosylvian sulcus," gives a fixity to the latter which it did not possess before; and the result is the Sylvian fissure, or, to be strictly accurate, part of the posterior limb of the fissura Sylvii.

In the general review of the condition of the sulci in the Mammalia, it was noted that in the Rodent *Dolichotis* and in the Edentate *Myrmecophaga* a peculiar union of the suprasylvian and pseudosylvian sulci occurs. In the light of the foregoing discussion, these facts may be simply expressed by the statement that these two mammals have a Prosimian Sylvian fissure.

If, after carefully studying the arrangement of the sulci in the Eluroid and Cynoid

\* E. A. Schäfer, 'Text-Book of Physiology,' vol. ii. 1900, fig. 333, p. 734, fig. 335, p. 735.

† 'The Anatomy of the Central Nervous System,' American translation, 1909, p. 225.



Carnivores, the student next examines the brain in the Arctoidea, he will find that the whole of the first arcuate gyrus of Leuret has become submerged in a great cleft in the situation of the pseudosylvian sulcus, and that there is a pronounced tendency for the anterior limb of the second arcuate gyrus to become submerged. This tendency, which is seen in most Bears, becomes more marked in *Meles*; and in most of the Seals the whole of the anterior limb of the second arcuate gyrus and the greater part of the suprasylvian sulcus become swept into the pseudosylvian cleft. There is therefore in the Arctoid Carnivores a tendency to the production of a condition which is analogous to, without however being altogether identical with, the state of affairs which has already become evolved in the Primates. It is of interest to note that when the suprasylvian sulcus is swept into the pseudosylvian sulcus in *Otaria*, *Odobenus* [*Trichechus*], and *Phoca*, it becomes separated from the postsylvian sulcus (to which it is united in most Carnivores). When the suprasylvio-pseudosylvian complex is formed in *Myrmecophaga*, the postsylvian sulcus becomes disconnected; but in the anomalous case (*vide supra*) in which the suprasylvian sulcus is not joined to the pseudosylvian, the former sulcus was joined to the postsylvian.

These peculiar phenomena are of great interest in the interpretation of the Prosimian brain. It has frequently been noted in this memoir that in the Prosimia, and especially in the genus *Lemur*, the mode of ending of the upper extremities of the suprasylvian and pseudosylvian sulci is exceedingly variable, and indubitably points to a connection between these two furrows, which has only recently been broken. In the peculiarly interesting brain of *Chiromys*, the suprasylvian and the variable pseudosylvian sulci are widely separated, as in most quadrupeds; and, like the parallel case afforded by the aberrant brain of *Myrmecophaga*, the suprasylvian sulcus then becomes joined (in most cases) to the postsylvian sulcus.

The extreme variability of the postsylvian sulcus in *Chiromys* is chiefly the result of the peculiar inconstancy of the pseudosylvian sulcus; for it will be obvious, from an examination of the brains of *Procararia* and the Ungulata, that the characters of the postsylvian (which is a morphologically unstable sulcus) are determined chiefly by the nature of the pseudosylvian sulcus. The irregularity of the postsylvian sulcus may also be partly due to the fact that *Chiromys* has obviously been subject to marked retrogressive changes.

In most Lemurs the postsylvian sulcus is a simple linear furrow, which obviously represents the parallel or superior temporal sulcus of the Apes and Man.

Although the pseudosylvian sulcus has a morphological importance and stability which are immeasurably less than that of the suprasylvian sulcus, it is obvious that it is the former which is the chief determinant of the peculiar "Sylvian formation." That this is so is shown by a study of the Carnivora, in many of which (as, for instance, in many Canidæ, the larger Felidæ, and Hyænidæ) a condition so spuriously like that of the true Sylvian fissure is produced without any participation by the suprasylvian sulcus, that the mistake of regarding the Carnivore pseudosylvian sulcus and the Primate Sylvian fissure as homologues is not unnatural. The suprasylvian sulcus, however, adds stability to a region which in other mammals is notoriously variable and fickle. The

upper [or caudal] part of the "Sylvian fissure" is purely suprasylvian, but the lower [or anterior] part of the sulcus is formed by the meeting of the dorsal lip of the suprasylvian sulcus with the ventral lip of the pseudosylvian sulcus.

In many Prosimian brains, especially of the genera *Lemur*, *Propithecus*, and *Indris* (but also, to a less marked degree, in *Galago*, *Perodicticus*, and *Nycticebus*), the lower end of the suprasylvian sulcus may be seen emerging from the "Sylvian fissure" some distance above the rhinal fissure. Several writers have noticed this. Ziehen, for instance, calls it the "Vorderster Abschnitt der Fissura circularis externa (s. Reilii)" (Arch. f. Psych. Bd. xxviii. p. 929).

These relations of the pseudosylvian and suprasylvian sulci are identical with those found in the smaller Cebidæ and Cercopithecidæ; but in these Monkeys the lower end of the suprasylvian sulcus is not exposed. It begins to emerge in the *Cynocephali* and *Semnopithecii*, and in *Hylobates* and the Anthropoid Apes it becomes prolonged forward (as the "opercular sulcus" of Marchand) so as to almost meet the fronto-orbital [diagonal] sulcus. Even in the Simiidæ the dorsal lip of this forward extension of the suprasylvian sulcus and the anterior lip of the diagonal sulcus tend to become opercular, and extend downward and backward until in most human brains they meet the opercular caudal lip of the pseudosylvian sulcus, and thus completely cover the anterior insular area, which is always exposed in non-human brains. In Man alone is the Sylvian fissure complete. In the Apes the "stem" of the fissure is sometimes formed, but the so-called Sylvian fissure of Monkeys really represents only a part of the posterior limb of the human Sylvian fissure. The fully formed anterior limbs are never found, except in the brain of Man.

The extent of submerged area varies considerably in the different Prosimian genera. In *Lemur* there is a very considerable area, chiefly overlapped by the opercular lip of the pseudosylvian sulcus: in *Tarsius*, *Microcebus*, and *Nycticebus* there is practically no submerged area, so that if the term "insula" be used as synonymous with "overlapped neopallium," the opinion of Flower and Ziehen that there is an insula in *Lemur* but not in *Nycticebus* is justified.

But it has been demonstrated that in the Apes a considerable part of the insula is not submerged and extends forward as far as the fronto-orbital sulcus. If my identification of the latter sulcus in the Lemurs is correct (and in this matter I am supported by the opinion of Ziehen and Flatau and Jacobsohn), the insula must be regarded as being exposed in a very considerable part of its extent. We have no certain criterion to inform us which neopallial areas should be regarded as "insula." In the human brain the insula is that area of neopallium (1) which is submerged in the Sylvian fissure, (2) is circumscribed (almost completely) by limiting sulci, (3) is applied to the lateral aspect of the nucleus lenticularis, and (4) is split to form a claustrum. If we adopt any of these criteria in the Lemurs, the region so mapped out will fulfil none of the other three conditions.

The next group of sulci to be considered includes the lateral, coronal, and crucial.

The sulcus which I have called "lateral" in the Lemurs is regarded by Ziehen as the representative of the "Bogenfurche" of the Dog's brain, which is composed of the

lateral, ansate, and coronal sulci \*; the sulcus which I distinguished as "coronal" he regards as the prorean; and he agrees with me in the recognition of the sulcus *f* as part of the central sulcus. The latter sulcus is considered by Flatau and Jacobsohn† to represent the superior precentral sulcus, because it occupies a position in relation to the intraparietal sulcus analogous to that which is presented in the brain of Apes.

I shall discuss first of all the representation of these sulci in the general body of mammals, and then follow the evolution of the corresponding furrows in the Apes.

If we follow the example of Ziehen, and limit our mammalian horizon to such specialized Carnivores as *Canis* and *Phoca*, neglecting all the generalized Carnivores and the Ungulates, Edentates, and Rodents, we might perhaps arrive at the same conclusion and regard the sulcus I have called "lateral" as the homologue of the conjoint coronolateral furrow of many Carnivores. If, however, we study the developmental tendencies not only in one or two specialized forms, but in the whole Mammalia (in such a manner as I have roughly sketched out already), the whole evidence will point to the conclusion that the sulci which I have called "lateral" and "coronal" respectively are in reality the homologues of the sulci of the same names in *Viverra*, *Procyon*, and all mammals. In other words, the coronal sulcus, instead of being represented in the furrow which I have called "lateral," as Ziehen would have us believe, really exists in the Lemurs as the separate sulcus which I have called "coronal." The latter sulcus (Ziehen's  $\zeta$ ) is regarded by the same writer as the homologue of the prorean.

The prorean sulcus has a peculiar distribution in the mammalian series. It is seen in both the Polyprotodont (*Thylacinus*) and Diprotodont Marsupials (*Macropodidæ*, *Phascolumys*, and extinct *Thylacoleo*), in *Myrmecophaga* and *Orycteropus* alone of the Edentata, and reaches the height of its development in the Carnivora, and especially in some of the Arctoidea, such as *Gulo*. If we seek for this sulcus in the more generalized Carnivora, and especially the Viverridæ, no such separate element as the prorean sulcus will be found. In the Viverridæ the coronal sulcus is prolonged forward so as to take the place, functionally, if not morphologically, of the prorean sulcus.

A similar phenomenon occurs in most Ungulates, and in the generalized Hyrax (*Procavia*) the coronal sulcus extends far forward on to the apex of the hemisphere. Much light is thrown upon this perplexing problem by a comparison of the arrangement of these sulci in certain Rodents and Edentates with that found in other mammals.

In the Carnivora the coronal is separated from the prorean sulcus by a mesial extension of the orbital (presylvian) sulcus. This prolongation is certainly a purely mechanical phenomenon; *i. e.*, the tension of the growing cortex becomes relieved by the extension of a pre-existing furrow, which in this case is the orbital. In *Orycteropus*, and sometimes in *Myrmecophaga*, the mesial prolongation of the orbital is united not only with the prorean but also with the anterior end of the coronal sulcus. In the brain of *Dolichotis* (Rodentia) the orbital sulcus is not prolonged beyond its morphological limits (if such a phrase is permissible), but the coronoprorean complex retains a form which is curiously reminiscent of the united coronary and prorean sulci in *Orycteropus*. This

\* Arch. f. Psychiat. Bd. xxviii. p. 921.

† Handbuch, p. 178.

would seem to indicate that the "coronal" sulcus of the Viverridæ, of the Ungulata, and of the Lemurs ought properly to be regarded as prorean-coronal. For the constant development of the prorean sulcus in those brains (of such widely separated mammals as the Marsupials, Edentates, and Carnivores) in which its union with the coronal sulcus is prevented by a "mechanical" extension of the orbital seems to indicate that the prorean sulcus possesses some definite individuality and morphological stability.

In the brain of *Chiromys* there is a peculiar modification of this region (which shows unmistakable signs of retrogressive change). In some cases there is a definite typical orbital sulcus and, in a more dorsal position, another sulcus which is obviously the anterior part of a coronal (or prorean-coronal) sulcus which has become broken into two fragments, like that of *Nycticebus*. In other cases the two sulci (*i. e.* the orbital and the anterior fragment of the prorean-coronal complex) become united. Oudemans calls this sulcus simply "prorean." I think that Oudemans's and Ziehen's use of the term "prorean," without being absolutely erroneous, fails to express the whole truth.

There can be no difficulty in interpreting the sulci lateralis and coronalis in terms which are applicable to the Apes, because these two sulci (in the form seen in the genus *Lemur*) are exactly reproduced in some of the smaller Cebidæ, such as *Callithrix*. The lateral sulcus becomes the intraparietal (or "interparietal," as the Germans call it) sulcus; and the coronal sulcus is identical with that variously termed "*frontalis principalis*," "*rectus*," "*rostralis*," among many other designations. It includes the representatives of the two sulci called respectively "*rectus*" and "*arcuatus*" in the Apes. The latter certainly represents the inferior precentral sulcus of the human brain; whereas the homology of the former is the subject of great divergence of opinion. Hervé, Eberstaller, Waldeyer, Giacomini, and Dubois\* consider that the sulcus rectus becomes the sulcus frontalis medius of Eberstaller in the human brain; whereas Cunningham and Marchand incline to the old view of Gratiolet, that it represents the sulcus frontalis inferior. As I have shown in the above notes that the fronto-orbital sulcus (which Waldeyer, Giacomini, and their school regard as the homologue of the inferior frontal sulcus) is certainly the anterior limiting sulcus of Reil, the evidence seems to point to the view of Cunningham and Marchand as the true interpretation.

The postlateral sulcus is as variable in the Lemurs as its representative in the Carnivora and other mammals is unstable. Beddard, Ziehen, and Flatau and Jacobsohn call it parieto-occipital; Chudzinski labels it "occipital," a term which is apparently applied in the same way as "parieto-occipital" used by the other writers. Beddard further complicates matters by applying the term "Simian" [*i. e.* Affenspalte] to it in *Nycticebus* (Proc. Zool. Soc. 1895, p. 144).

In the discussion of the mesial surface of the hemisphere it is shown how misleading and erroneous it is to call this furrow "parieto-occipital."

The postlateral sulcus undoubtedly becomes the sulcus occipitalis transversus of Ecker in the Apes and Man.

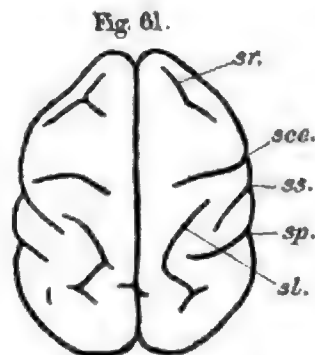
\* "*Pithecanthropus erectus*," Proceedings of the Fourth International Congress of Zoology at Cambridge, 1898 (published 1899), p. 83.

It is unnecessary to enter any further into the discussion of the later evolution of this sulcus in the Apes, for my views on this subject have been far more aptly expressed than I am capable of stating them, in Cunningham's monograph \*. There still remains for discussion the most difficult problem in the interpretation of the Prosimian sulci, *i. e.* whether the central (Rolando's) sulcus is represented in any form in the Lemurs.

The central sulcus is easily recognizable in all the Simiidae and Cercopithecidae. Nor can there be much uncertainty concerning its identity in the larger Cebidae. If the smaller Cebidae be studied without comparison with the larger members of the family, it may seem very doubtful whether the small central sulcus in such a form as *Chrysotrrix* (for example) might not really represent the ramus postcentralis of the intraparietal sulcus. But an examination of the brain in the whole Family shows that the postcentral sulcus first appears long after the central itself is fully formed. So that in those Cebidae in which only one sulcus is present in the appropriate place, it may be regarded as the central.

The simplest form of a well-defined central sulcus may be seen in the genus *Pithecia* as a simple transverse sulcus in the interval between the intraparietal and "coronal" sulci.

In the genus *Callithrix* there is sometimes no trace of a central sulcus; in other cases there is merely a shallow depression in front of the intraparietal sulcus, and the situation



*Pithecia*.—Dorsal aspect of brain. Nat. size.

where one would look for the upper end of the central sulcus; in other cases again there is a small transverse furrow in this situation.

Beddard represents this sulcus in its best-developed form in the brain of *Callithrix torquata* †, and calls it precentral.

The brain of *Callithrix* is of peculiar interest to the student of the Prosimian organ, because the arrangement of the sulci on the outer surface of its cerebral hemisphere exactly reproduces that found in the Lemurs, as Sir William Flower forty years ago

\* D. J. Cunningham, "Surface Anatomy of the Primate Cerebrum," 'Cunningham Memoirs,' No. VII. Royal Irish Academy, 1882, p. 221.

† "On certain points in the Anatomy of *Callithrix torquata*," *Novitates Zoologicae*, vol. viii. October 1901, pl. xi. fig. 5 (dorsal aspect, wrongly labelled "mesial").

showed. The Sylvian, "lateral," "coronal," postsylvian," and orbital are quite lemuroid in position and constitution. The presence of the small and variable sulcus in front of the intraparietal [lateral] sulcus completes the resemblance.

The possibility of recognizing a central sulcus in the Lemurs has recently been discussed by Beddard\*, who believes that "the lemurs are to be differentiated from the higher primates by the fact that their brains do not exhibit any trace of a fissure of Rolando [central sulcus], so constant a feature of all monkeys and apes." To justify the latter statement he regards the anterior extremity of the intraparietal [his "supra-angular"] sulcus as the representative of the central sulcus, chiefly because it "is in an ideal position for a fissure of Rolando"; *i.e.* it is midway between the anterior and posterior poles of the hemispheres, which according to Beddard is the position of the central sulcus in the genera *Ateles*, *Myceles*, *Cebus*, *Brachyurus*, and *Lagothrix*. This argument, however, is quite fallacious because it ignores the fact that a relatively enormous increase in the extent of the pallial area in front of the Sylvian fissure occurs within the family Cebidæ, so that in the lowlier members of the Family the central sulcus, if present, must be placed relatively much further forward in the hemisphere than it is in the larger genera. An indication of such a tendency is exhibited in the brain of *Pithecia*.

In the earlier memoir of Ziehen a very different interpretation of the homologies of these sulci is suggested; and Beddard makes no attempt to refute these arguments. Ziehen regards the sulcus which is found in front of the lateral sulcus in *Perodicticus* as the central; he also considers that in *Nycticebus* the central sulcus is represented by the two sulci *f* and *x + y*. The sulcus *f* in the genus *Lemur* is considered by Ziehen to represent the central sulcus or the upper portion of it, whereas Flatau and Jacobssohn† anticipated Beddard in regarding it as "precentral." These writers then proceed to criticise the argument of Ziehen that the furrow *f* represents the central sulcus, because it occupies the appropriate position in regard to the lateral (intraparietal) sulcus. They argue that the sulcus in question might with equal justice be regarded as the superior precentral by reason of its relationship to the coronal (their sulcus "frontalis"), utterly ignoring the fact that the precentral sulcus never occurs in the absence of the more stable central sulcus.

They further urge, in opposition to Ziehen's suggestion, the T- or Y-shape of the sulci, their sagittal direction, and the fact that, according to Chudzinski's diagram, there is a sulcus resembling the supposed central sulcus of *Lemur* in front of a definite central sulcus in the brain of *Indris*. They summarize their criticism of Ziehen's conclusions regarding the central sulcus in these words:—"Die Möglichkeit, dass der untere der beiden queren, hinter dem Sulcus frontalis [coronalis] gelegenen Furchen [*i.e.* the sulcus *e* of *Lemur* and the sulcus *x + y* of *Nycticebus*] homolog dem Sulcus centralis der Affen ist, lässt sich mit absoluter Sicherheit nicht bestreiten, wenn auch die Gestalt und Lage der Furche mehr dem Sulcus præcentralis (arcuatus) entspricht; die obere [sulcus *f*] der beiden queren Furchen ist aber sicher ein Homolog des Sulcus præcen-

\* 'Novitates,' 1901, p. 365.

† 'Handbuch,' p. 178.



tralis superior, da sie bei den höchsten Arten der Halbaffen genau wie bei den wahren Affen zwischen Sulcus frontalis (principalis) und Sulcus centralis gelegen ist" \*.

It will be seen, therefore, that there is little semblance of agreement with regard to the central sulcus in the three most recent memoirs on the Prosimian brain.

There is no necessity to again review all the data afforded by a study of the genera *Lemur*, *Nycticebus*, *Perodicticus*, *Propithecus*, and *Chiromys*. It is sufficient to recall that a very pronounced tendency is exhibited in these varied forms for the small sulcus *f* to fuse with the caudal extremity (*e*) of the coronal sulcus, with the resulting formation of a great transverse sulcus, which can be nothing else than the central sulcus of the Primates.

#### ON THE AFFINITIES OF THE LEMURS.

It does not come within the scope of this work to consider in all its bearings the vexed question of the relationships of the Lemuroidea. It would, indeed, be presumptuous to attempt such a difficult task, which has baffled many zoologists with the best equipment for performing it. All that I am concerned with at present is the setting forth of such evidence as the brain affords, and the determination of its value as an index of the affinity of its possessor to other mammals.

The greatest divergence of opinion exists among zoologists as to the relative closeness of the bonds which link the Lemurs and the Apes.

Many writers, such as Gervais and Milne-Edwards, have relegated the former to an Order quite distinct and separate from the Apes; and Flower virtually, though not nominally, subscribes to the same opinion, for he retains the Lemurs among the Primates chiefly in deference to "the traditional views of zoologists." On the other hand, Linnæus, Lesson, Huxley, Broca, and Mivart assign them a subordinate rank in the Primates. Nevertheless Mivart, who is generally quoted as a champion of this view, has stated "that the differences between the apes and lemurs are so many and so great, that it cannot be considered otherwise than in the highest degree improbable that (on the evolutionary hypothesis) they took origin from any common root-form that was not equally the progenitor of other mammalian Orders" †. So that Mivart also virtually places himself in the ranks of those who favour a separate ordinal rank for the Lemurs.

Dr. Forsyth Major's careful studies of the skeleton and teeth of the recent Lemurs, and of an interesting series of extinct Lemuroids, within the past few years, have utterly stultified Flower's statement that "as a more complete knowledge of their organization has been gradually attained, the interval which separates them structurally from the monkeys has become gradually more evident." Forsyth Major's conclusion is so diametrically opposed to Flower's teaching that, to quote his own words, his "position . . . will have to be expressed in classification by giving up the two separate suborders of Primates, thus going one step further than Mivart" ‡.

\* Flatau and Jacobsohn, 'Handbuch,' p. 178.

† Article "Ape," Encyclopædia Britannica.

‡ "Summary of Present Knowledge of Extinct Primates from Madagascar," Geological Magazine, n. s., Decade 4, vol. vii, November 1900, pp. 492-499.



It is hardly necessary to insist on the value of cerebral characters as an index of the affinities of the animal, when it is recalled that the mammalian brain is perhaps the only organ which can be truly said to represent in itself the whole organism. For even though the brain is responsive to changes of habit in the animal, and innumerable other factors which in various ways influence the proportions of its various parts and modify its shape, yet, in its essential plan, it is perhaps the most conservative organ in the whole body. Thus the same fundamental plan of the brain is found throughout the Eutheria, and, with the exception of the striking changes in the constitution of the cerebral commissures, it is common also to all the Metatheria. In the foregoing notes I have attempted to show that underlying the exceedingly variable and apparently haphazard disposition of the sulci of the cerebral hemisphere—which, being the most recently-modified, are consequently the most changeable regions of the brain—there is a fundamental group of homologous furrows, which are the common property of the whole Meta- and Eutheria rather than the exclusive distinction of one Order.

The fact of having thus discarded as obsolete and unjustifiable the belief that each Order of mammals evolves for itself a number of furrows which are incapable of being homologized with those of other Orders, may seem to have broken down the barriers which separate the Lemurs from other mammals (for even those who have most magnified the differences between Apes and Lemurs have been compelled to adopt from the higher Primates their nomenclature for the Prosimian sulci). But this is by no means so. For, having demonstrated the identity of the various elements which may unite in various manners to form the most heterogeneous series of patterns in the different Orders, we are the better able to appreciate the Ordinal value of these varied groupings of the series of sulci, the morphological values of which we know, than we should if a new set of features of unknown importance were evolved in each Order.

It surely does not lessen the great systematic importance of the fact that the calcarine and suprasylvian sulci behave in a very peculiar and identical manner in the Lemurs and Apes, to know that the direct homologues of these furrows are disposed in a strikingly different manner in the various other mammalian Orders. On the contrary, the fact that the different patterns are composed of such stable elements enhances the value of the plan of the sulci as an index of relationship.

The peculiar constancy of the arrangement of the calcarine, retrocalcarine, and paracalcarine sulci is alone sufficient to indicate the close bonds of affinity which unite all the Lemurs, and even such different members as *Tarsius* and *Chiromys*, and at the same time separate them from all other mammals.

The confluence of the calcarine and retrocalcarine sulci is peculiarly distinctive of the Primates, and in this respect the Lemurs conform to the Ordinal type. In many of the New-World Apes the paracalcarine sulcus is much less perfectly developed than it is in the Lemurs; and in this respect the latter closely resemble the highest Apes, in which the paracalcarine sulcus forms the ventral element in that peculiar combination of two sulci which is commonly distinguished as "parieto-occipital." In making this statement I am not unmindful of the probability that this type of paracalcarine sulcus may be merely its most primitive form.

The arrangement and behaviour of the sulci on the outer aspect of the hemisphere closely follow those of the Ape, and especially of the lowlier Cebidæ. There is the same peculiar form of suprasylvian sulcus merged in the Sylvian fissure in both Families. The lateral sulcus is closely similar, as in fact it is in all mammals, but it shows a peculiar tendency, which is exhibited in *Nycticebus* in the Lemurs and in *Chrysothrix*, *Nyctipithecus*, and *Myocetes* in the Cebidæ, to become concurrent with the suprasylvian (Sylvio-intraparietal union), which is a striking instance of the wide separation of the Primates from all other mammals (in most of which the first stage of this process, *i. e.* the pushing, as it were, of the suprasylvian sulcus on to the pseudo-sylvian sulcus, has not begun, so that the further stage of pushing the lateral sulcus into the Sylvian complex is not even possible); at the same time it is a further testimony to the affinity of the Lemurs and the Cebidæ.

So far as the other sulci—the coronal, the orbital, the diagonal (fronto-orbital), the central rudiment, the postsylvian, and the postlateral—are concerned, there is the closest identity between all of these in the Lemurs and such lowly Cebidæ as *Callithrix*, the importance of which is again enhanced by the contrast afforded by the behaviour of their respective representatives in other mammals.

There is no sulcus, perhaps, more distinctive of the Primates than the normally-constituted central (Rolando's) sulcus. Such a sulcus (as a unit) is not found in any other Order of mammals; but there is a widespread tendency in the Lemurs—in *Perodicticus* of the Lorisinæ, in certain cases in *Propithecus*, and in *Chiromys*—to the development of this characteristic sulcus.

The fronto-orbital sulcus, which, like the paracalcarine, is absent in many New-World Apes, is often as fully developed in the Lemurs (*Lemur*, *Propithecus*, and *Indris*) as it is in the larger Cercopithecidæ. And even if this furrow (as in the analogous case of the paracalcarine) is represented among the other mammals (in the diagonal sulcus), it is still important that a furrow which is not present in many New-World Apes should occasionally develop in the Lemurs in the same situation and have the same form as the fronto-orbital sulcus in the larger Apes.

The degree of affinity of one mammal to another is a purely relative matter, which it is difficult to express adequately. But if we take all the features of neopallial sulci into consideration, it can confidently be stated that, judged by the standard of the other mammalian subdivisions, the differences between the brain in the Lemurs and such Primates as the Cebidæ are certainly not worthy of being granted either Ordinal or even Subordinal importance.

The differences between the brain in the Edentate Families Myrmecophagidæ, Dasypodidæ, and Bradypodidæ (which we recognize to be united by bonds of affinity) are considerably greater than those which divide the Lemurs and Cebidæ. Or, to adopt a more certain or, at least, more generally recognized scale of relationships, there is a much closer resemblance between the brain in the Lemurs and Apes than there is between those of the Æluroid and Arctoid Carnivores.

So far as the neopallial furrows are concerned, the Lemurs might be regarded as inseparable from the Cebidæ, if it were not for the fact that the other parts of the brain exhibit very definite distinctive features.

The brain of a Lemur is relatively smaller and more macrosomatic than that of an Ape. In addition, there are differences in the so-called occipital region.

The data for comparing the size of the brain in the Lemurs with other mammals are unfortunately somewhat scanty, and (if we neglect the wholly unreliable figures yielded by weighing organs which have been modified by the action of preservative agents) are almost wholly the result of the careful investigations of Professor Max Weber of Amsterdam †.

The weights recorded by Weber ‡ are as follows :—

SPECIES.	Brain-weight.	Proportion to Body-weight.
<i>Lemur varius</i> , Geoff., ♂ .. . . .	33	1 : 103
" " " ♀ .. . . .	28.7	1 : 75
* " " " ♂ .. . . .	39	1 : 74.3
<i>Lemur mongoz</i> , Linn., ♀ .. . . .	28	1 : 76
" " " ♀ .. . . .	21.1	1 : 60
<i>Nycticebus tardigradus</i> , Gray, ♂ .. . . .	8.18	1 : 61
" " " ♂ .. . . .	7.72	1 : 54
<i>Perodicticus potto</i> , Lesson .. . . .	9.3	1 : 76
" " " .. . . .	13.25	1 : 57
" " " .. . . .	9.59	1 : 76
<i>Chiromys madagascariensis</i> , Geoff., ♀ .. . . .	42.95	1 : 37

The record of the weight of the brain in *Chiromys* is identical with that of Oudemans (Natuurk. Verh. Kon. Akad. Amst. xxvii. 1890, p. 27).

As the result of an elaborate series of investigations, Professor Eugène Dubois arrived at the conclusion that "in the Lemuridæ, *Nycticebus* and *Tarsius* occupy the same degree on the scale of brain development as measured by its quantity," and further that "this is about equal to that expressed by the lower indices in the Ungulata and Carnivora" §. In the same place, however, it is stated that "the lower Old-World apes . . . do not distinctly exceed in this respect the Ungulata and Carnivora."

In Ziehen's tables there are three records (all by Max Weber) of brain-weights in the Hapalidæ, ranging from 9.8 grm. (1 : 20) to 12.8 grm. (1 : 26); and three records in the genus *Pithecia* (two by Flower and one by Weber), showing a variation of 22 grm. (1 : 20) to 36.2 grm. (1 : 15) in the brain-weight. These numbers are sufficient to show how much more richly the New-World Apes are endowed with brain-substance than the Lemurs are.

Dubois's statement concerning *Nycticebus* and *Tarsius* presumably does not apply to

† 'Vorstudien über das Hirngewicht der Säugethiere,' Leipzig, 1896.

Other records have been published by Burmeister, Bischoff, Flatau and Jacobsohn, and Ziehen, but the weights are not those of fresh brains and cannot be corrected with any accuracy.

‡ All these weights except that marked with the asterisk (\*) are quoted from Bardeleben's 'Handbuch der Anatomie des Menschen,' Nervensystem (by Prof. Ziehen), p. 368.

§ "On *Pithecanthropus erectus*," Proc. 4th Intern. Congr. Zool., Cambridge, 1898, p. 91.

the Lemurs as a whole. If we examine the few records which are quoted above, and compare them with data obtained from other mammals in exactly the same manner by the same investigator, it will then be seen from a comparison of the body-weights of those non-Primate mammals which possess the same absolute brain-weights as various Lemurs, that the proportion of brain to body is considerably higher in the latter.

Compare the series of brain-weights in the genus *Lemur*, which vary from 21·1 grm. to 39·1 grm. (representing the following proportions of brain to body:—1 : 60, 1 : 75, 1 : 76, 1 : 84, and the exceptional 1 : 103), with the following measurements of Carnivora:—

SPECIES.	Brain-weight.	Proportion to Body-weight.
<i>Viverra zibethica</i> , Gray. ....	30·2	1 : 103
<i>Felis catus</i> , Linn. ....	39·6	1 : 105
<i>Felis domestica</i> , Gm. ....	33·5	1 : 10 { the highest of
"    "    "    "    "    "    "    "	32	1 : 128 { 7 measurements.
<i>Canis lupus</i> , Linn. ....	31	1 : 205 }
"    "    "    "    "    "    "	39·1	1 : 84 }
<i>Paradoxurus musanga</i> , Gray ....	22	1 : 141
<i>Galictis vittata</i> , Schreb. ....	21·1	1 : 91
<i>Herpestes albicauda</i> , Cuv. ....	23·1	1 : 81

In all of these Carnivora the proportion of the brain-weight to the body-weight is less (and in many cases very considerably so) than it is in Lemurs with brains of a corresponding size. And in other mammalian Orders the disproportion in the size of the body per unit of brain-weight is even more pronounced. The Lemurs all have relatively large brains in comparison with other mammals, but are much more poorly endowed in this respect than the Apes.

The data are too scanty to enable us to decide whether this difference in the brain-weights of Apes and Lemurs is due merely to the failure of the latter to keep pace in brain-growth with the former, or is the result of an actual reduction in size.

The most noteworthy distinction between the brain of the Lemurs and the Apes is the relative size of the olfactory regions of the brain.

The brain of the Apes is distinctly microsmatic. The olfactory bulb is very small, and is borne on a long attenuated peduncle; the anterior part of the pyriform lobe is so reduced as to be recognizable with difficulty, and the posterior part is so small that it is almost always confined to the ventro-mesial aspect, and rarely extends on to the lateral aspect of the hemisphere; and the hippocampus is relatively very small.

In mammals the size of the olfactory parts of the brain is subject to great variations.

Thus in all aquatic mammals they become greatly reduced in size (*e. g.* in *Ornithorhynchus*, the Pinnipedia, the Sirenia, the Cetacea), or even entirely absorbed (in the Odontoceti). In mammals which lead an arboreal life they are relatively smaller than in those which lead a terrestrial existence, *e. g.* the rhinencephalon is relatively much

smaller in the arboreal *Cycloturus* than in the terrestrial *Myrmecophaga*, two Edentates of the same family; but it is the peculiarity of the Apes that they have become extremely microsmatic for no apparent reason, the diminution of their olfactory organs being much more pronounced than it is in any other arboreal animal. This phenomenon is undoubtedly to be mainly attributed to the increasing efficacy of the neopallium as an "organ of mind," and its consequent usurpation of the rôle of guiding the creature, which elsewhere among mammals is fulfilled chiefly by the sense of smell.

It is a very significant fact that the Lemur which exhibits evidence of being the most primitive—*Tarsius*—possesses the most extensive occipital prolongation, and is more microsmatic than any other of the Prosimiæ. Thus the olfactory bulb of *Tarsius* is only half as large as that of *Microcebus*; and yet the former is appreciably greater than that of *Midas*.

The importance which has been attached to the amount of cerebellum covered by the cerebral hemisphere as an index of the degree of brain-development is altogether disproportionate to its true significance. By this I do not mean to imply that the degree of caudal prolongation of the hemisphere is not a very important indication of the size of the cerebral hemisphere, but it must not be forgotten that it is merely one of several indications of the degree of cerebral expansion. The failure of the cerebral hemispheres to completely overlap the cerebellum is an obvious point of distinction between the brain of the Lemurs and most Apes. In the Lemurs the extent of the backward prolongation of the hemisphere varies considerably. In *Nycticebus*, for example, there is only a very narrow strip of cerebellum uncovered. In the Galaginæ and in *Tarsius* the extent of the caudal prolongation of the hemisphere is perhaps greater than in any other Lemur; i. e., if its dimensions are estimated in relation to the position of the corpus callosum and by the size of the calcar, rather than by the situation of the caudal pole of the hemisphere with relation to the cerebellum. The relative greatness of the occipital extension of the hemisphere in these particular forms is all the more significant, because *Tarsius* and *Galago* are the Lemurs which have probably become least changed (so far as the brain is concerned) from the early Prosimian type. It is hence probable that the immediate ancestors of the Lemurs possessed brains of a more pithecoïd form. There are many other suggestive facts which point in the same direction.

In most mammals the calcarine and intercalary (? paracalcarine) sulci become continuous (probably for purely mechanical reasons), and it is hardly conceivable that the small caudal extension of the hemisphere in the recent Lemurs is sufficient to so completely dissociate the calcarine from the intercalary sulcus, and to lead to its confluence with the retrocalcarine sulcus, or in fact to supply the mechanical factors which call the latter sulcus into being. It is difficult to conceive of the present relations of the three sulci of the calcarine group having been produced except in a brain with a much more pronounced extension of the hemisphere than at present exists.

It has been shown by Prof. A. Milne-Edwards, and emphasized by Dr. Forsyth Major\*,

\* 'Novitates Zoologicæ,' vol. i. 1894, p. 33.

that in the young *Propithecus Edwardsi* the caudal extension of the cerebral hemisphere over the cerebellum is distinctly greater than it is in the adult. From an examination of the cranium of a young (15 days old) *Propithecus coronatus*, which Dr. Forsyth Major lent me, I have been able to establish this also for another species of a later age. However, in the brain of a young (15 days old) *Lemur fulvus*, which Captain Stanley Flower gave me, the cerebellum was exposed to as great an extent as in the adult. In different specimens of adult Lemurs, even of the same species, I have found considerable variety as regards the amount of cerebellum uncovered.

If we consider the marked disproportion in the size of the brain in the Lemurs and the Apes respectively, the possibility presents itself that the former may at one time have been much larger than it is now. If such were the case, it is certain that the process of reduction in size would be chiefly expressed in a curtailment of the caudal (occipital) prolongation.

A study of the peculiar series of variations in the Indrisinæ, *Chiromys*, and to a less extent in all other Lemurs, clearly shows that the hypothesis of a retrogressive change can alone explain this extreme variability.

It may be urged that it is not the mere retraction, so to speak, of the caudal pole of the hemisphere which distinguishes the occipital region of the Lemurs from that of the Apes, but also the absence of the posterior cornu in the former. This is a feature the importance of which has been grossly exaggerated. It is merely one of the expressions of a large neopallium, and the question of the presence or absence of the calcar and calcarine sulcus is not in any way involved in the issue. In any large mammal (large mammals being provided with actually, though not relatively, more extensive neopallia than the small) the increase in size of the neopallium may lead to the formation of a posterior cornu. We see this in the Carnivora, Ungulata, and Cetacea, as well as in the Primates. The Primates, being preeminent in neopallial greatness, naturally present in most cases a distinct posterior cornu.

The direct result of the "retraction" of the occipital extension of the hemisphere would be the obliteration of the posterior cornu.

The brain of *Tarsius*, which in most respects is so eminently Propithecoid, is distinguished from other Lemurs by the possession of a distinct posterior cornu indistinguishable from that of the smallest New-World Apes.

When it is recalled that the Eocene Lemuroids possessed brains no smaller in size than those of the recent forms (Cope), it would indeed be surprising if the brain should have remained stationary in size through all the succeeding ages.

So far as the brain is concerned, the Galaginæ are (with the exception of *Tarsius*) the most generalized of all the Lemurs. And, in view of the foregoing suggestions, it is not without significance that they also possess the most pronounced occipital prolongation.

The cerebral features of the members of the genera *Lemur* and *Haplemur* are not far removed from those of *Galago*. The peculiar variability in the extent of cerebellum covered by the cerebrum is suggestive of a "retraction" of the latter.

Far more specialized than these genera are the Indrisinæ, *Lepidolemur* being in most respects intermediate between the latter and *Lemur*. In different modes the Indrisine



type of brain is peculiarly specialized in the genus *Chiromys* and the extinct Lemuroid *Megaladapis*.

It is impossible, with any degree of accuracy, to place the peculiarly pithecoïd form of brain which *Globilemur* presents. So far as its characters can be determined, it resembles the type of the genus *Lemur* and the Galaginæ.

The Lorisinæ again present peculiar cerebral features. In many respects the brain is peculiarly simple, after the same manner as that of the Galaginæ. In *Perodicticus*, and to a less extent in *Nycticebus*, there is a peculiar tendency toward the formation of the typically Primate central sulcus.

*Tarsius* is obviously related, so far as the evidence of the brain is concerned, to the Galaginæ. This resemblance cannot be disguised even by the peculiar distortion of the brain in the former. It is in every respect distinctly Prosimian. But it also exhibits two interesting series of features. So far as the corpus callosum, the hippocampal formation, and the cerebellum are concerned, the brain of *Tarsius* conforms to the simplest Eutherian type, such as we find in the more generalized Insectivora—for example, *Erinaceus*. Yet its relative microsomatism (in comparison with other Lemurs), the proportion of its hemisphere which is placed on the caudal side of the corpus callosum, and the presence of a definite posterior cornu of the lateral ventricle, all indicate a nearer approach to the Simian condition than occurs in the brain of any other Lemur. *Tarsius* possesses at once the most generalized and the most pithecoïd brain of all the Lemuroidea.

In this connection it is interesting to quote some remarks concerning *Anaptomorphus* which were made seventeen years ago by E. D. Cope:—"The brain and its hemispheres are not at all smaller than those of the *Tarsius*, or of the typical lemurs of the present period. This is important in view of the very small brains of the flesh-eating and ungulate Mammalia of the Eocene period as yet known. In conclusion, there is no doubt but that the genus *Anaptomorphus* is the most Simian lemur yet discovered, and probably represents the family from which the anthropoid monkeys and men were derived" \*.

Zittel also has remarked that the Eocene Lemuroids (*Adapis*, *Microchoærus*) of Europe "combine features of the existing Lemurs and true Apes" †.

It is not easy to draw any certain conclusions from the evidence of the brain as to the relations of the Primates to other mammals.

The larger Carnivores show a tendency toward the development of a Sylvian complex like that of the Primates. There is a singular absence of any such tendency in the Ungulata. Like the latter, however, the Primates always retain a coronal sulcus, which in the main is nearer the horizontal than the vertical direction. It is a peculiar fact that the separation of the calcarine and intercalary sulci, which is so marked a feature of the Primates, should occur (practically) nowhere else in the Mammalia, except in the three Edentate families Myrmecophagidæ, Bradypodidæ, and Manidæ. In the case of

\* "The Lemuroidea and the Insectivora of the Eocene Period of North America," American Naturalist, May 1885, p. 467.

† Quoted by H. O. Forbes, 'Monkeys,' vol. i. p. 111.



the Anteaters there is another peculiar Primate feature: the suprasylvian and pseudosylvian sulci blend to form a Sylvian fissure. It is quite impossible to say how much importance is to be attached to such phenomena.

After seeking for some explanation for all the apparently conflicting features of the Prosimian brain, the following tentative working hypothesis as to the ancestry of the Lemurs shaped itself in my mind, and I insert it here merely as a slender bond connecting certain facts scattered through these notes.

The brain of the Primates was derived from some Insectivore-like type, the cerebral hemispheres of which attained a precocious development and, as one of the expressions of their greatness, bulged backward over the cerebellum. In consequence of this great extension of the "physical organ of the associative memory of visual, auditory, and tactile sensations," the sense of smell lost the predominance which it exercised in the primitive mammal (and in all the Orders of recent mammals), and the olfactory parts of the brain rapidly dwindled. This early Primate developed its distinctive type of calcarine sulcus and "Sylvian fissure," the lateral, coronal, and orbital sulci, and the characteristic central sulcus.

In the keen struggle for existence, the Lemurs ceased to keep pace with the other Primates so far as the increase in the size of the brain is concerned. They became more specialized, and their brain probably shrunk, thus leading to a retraction of the occipital pole of the hemispheres.

With the diminution of the size of the neopallium the sense of smell comes to play a more important part, and a secondary re-enlargement of the olfactory regions occurs. The blotting-out of the rhinal fissure may be an indication of this phenomenon.

This somewhat crude and tentative scheme is put forward to give expression to the view that the Lemurs are highly specialized Primates which share most of their brain-features in common with those of the Apes, and that some at least of the apparently primitive characters may be due to a secondary retrogressive modification of a more highly-developed type of brain.

#### ADDENDUM.—THE CEREBELLUM.

(Received April 24, 1902.)

In my account of the brain in the Edentata\*, I called attention to the fact (which had previously been recognized independently by Stroud and Kuithan) that underlying the apparently irreconcilable differences and seemingly divergent designs exhibited in the cerebellar architecture of mammals, there is one common fundamental plan which becomes variously elaborated in its details in different animals.

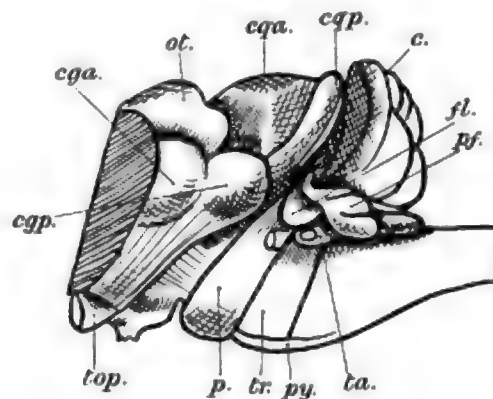
In attempting to describe the cerebellum in the Edentata I found that the nomenclature and mode of subdivision usually adopted in works on Human Anatomy were so ill-adapted to the needs of Comparative Anatomy, that it was quite impossible to describe

\* "The Brain in the Edentata," Trans. Linn. Soc. ser. 2, Zool. vol. vii. 1899, pp. 360 *et seq.*

the cerebellum of many mammals in the current terminology; and that even in the case of those which could be so described, the account would be altogether unnatural and hopelessly cumbrous. The chief reason for this is that the cerebellar fissure (*fissura horizontalis magna*), which is regarded in Human Anatomy of such fundamental importance as to be invariably taken as the starting-point in the primary subdivision, is a most insignificant cleft of quite secondary importance in most mammals, and is even absent altogether in others.

It therefore became necessary to seek some more stable line of demarcation between the various cerebellar regions. Accordingly I proposed a tentative scheme of subdivision based upon the recognition of the fissure called "preclival" as the primary natural line of separation of the mesial parts of the organ. My reason for adopting this fissure was the fact that it is present in all mammals, without exception, and is, moreover, the deepest fissure crossing the mesial plane. Ample confirmation of the justice and naturalness of this selection was afforded by the fact that two other investigators had independently come to the same conclusion—Stroud, as the result of a study of the development of the organ in the Cat and in Man, and Kuithan from embryological studies on the Sheep.

Fig. 62.

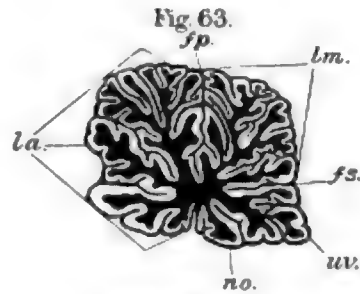
*Tarsius spectrum.*

Left lateral aspect of the brain-stem and cerebellum, exposed by cutting through the thalamo-striate junction and removing the cerebral hemisphere.  $\times 4$ .

When I examined the cerebellum in *Tarsius*, *Microcebus*, *Galago*, *Lemur*, *Nycticebus*, and *Chiromys*, it was not surprising to find that it conformed to the plan which has previously been shown to prevail among such divergent groups of mammals as the Ungulata, Edentata, and Carnivora. Yet I was not prepared to find within the Primates a form of cerebellum such as that of *Tarsius*, which so nearly approaches the most generalized mammalian type met with in the Insectivora, Marsupialia, the Dasypodidæ, and some Rodentia.

In the one Order we find therefore every gradation of cerebellar form, from the simplest and most generalized mammalian type to the most complex, though not the largest, example of cerebellar architecture. The undoubtedly close affinity of the different Primate genera enables us to speak with greater certainty of the apparent

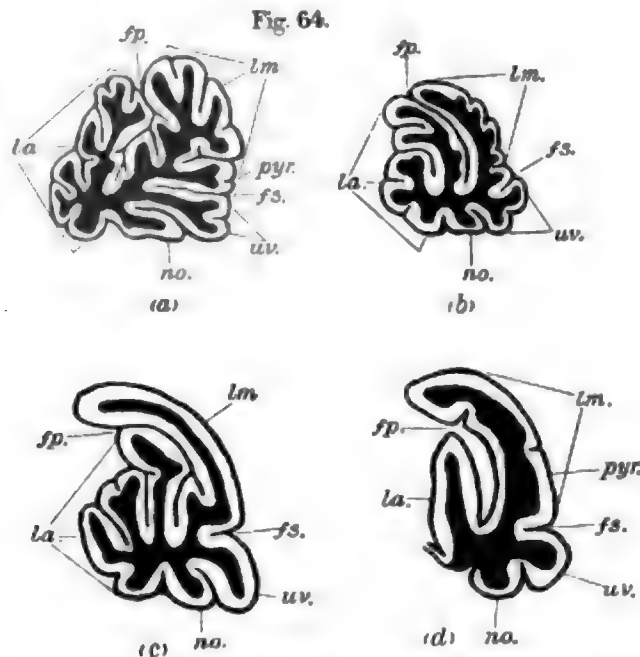
homologies of the various parts than was the case when I was discussing such widely separated mammals as the Edentates and Man.



*Lemur macaco.*

Diagram representing a mesial sagittal section of the cerebellum.  $\times 2$ .

The accompanying series of drawings (figs. 64a to d) representing mesial sagittal sections through the cerebellum in *Tarsius*, in the Insectivore *Erinaceus*, in the Marsupial *Perameles* (the pattern of which is identical with that of the Insectivore *Macroscelides*), and in the Marsupial *Notoryctes* (the simplest cerebellum in the Mammalia), will serve to indicate the different manner in which essentially the same pattern becomes elaborated in detail.



Diagrams representing corresponding sections in (a) *Tarsius*,  $\times 4$ ; (b) *Erinaceus*,  $\times 4$ ; (c) *Perameles*,  $\times 4$ ; and (d) *Notoryctes*,  $\times 8$ .

Such variations of the same simple plan might be adduced almost without limit from among the small Insectivora, Marsupialia, Chiroptera, Rodentia, and Edentata, but a comparison of *Tarsius* with a small Insectivore and a Marsupial will suffice to explain the general principle.

It will be seen that, in spite of its smaller size, the cerebellum of the Insectivore is slightly richer in furrows than the Marsupial, and that, in order to find in the former Order a cerebellar pattern of the same degree of richness as *Perameles* exhibits, we must select some small form such as *Macroscelides* or *Oryzoryctes*.

It will be seen that the pattern found in *Tarsius* is much richer in fissures than that of either the Insectivora or the Marsupialia. And, if it be objected that this contrast may be due to the smaller size of the organ in *Erinaceus*, the suggestion can be at once refuted by showing that in the larger Insectivore *Gymnura*, in *Galeopithecus*, in many Rodents like *Lepus*, and in the representatives of other Orders of a corresponding size, there is a greater poverty of fissures than there is in *Tarsius*. This fact might be more accurately stated by saying that the extent of the cerebellar cortex is determined, partly by the dimensions of the animal and partly by its zoological rank.

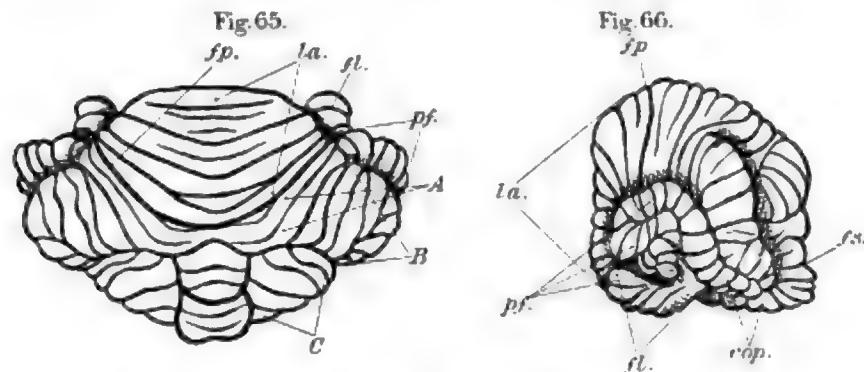


Fig. 65.—*Lemur macaco*. Dorsal aspect of the cerebellum.  $\times 2$ .

Fig. 66.—*Gazella dorcas*. Left lateral aspect of the cerebellum.  $\times 2$ .

The mesial part of the cerebellum is divided into three regions by means of the deep fissura prima, *pf.*, and by the shallower fissura secunda, *fs.* (fig. 64). The region in front of the fissura prima (which is homologous with the so-called "preclival" fissure) may be called the anterior lobe, that between the fissura prima and the fiss. secunda the central, or, better, middle lobe; the third region being the posterior lobe. The anterior and middle lobes may be quite simple undivided folia, as in *Notoryctes*, but the posterior lobe is always subdivided into two lobules, which correspond to the parts called "nodulus" and "uvula" respectively in Human Anatomy.

A comparison of a series of mammalian cerebella clearly shows that the posterior lobe does not increase in size to so marked a degree as the anterior and especially the middle lobe do; and, conversely, the ultimate subdivision of this lobe is evident at a much earlier phase in the phylogenetic history than that of the other two lobes.

The most noteworthy feature of the mesial section of the cerebellum in *Tarsius* is the plumpness and relative greatness (*i. e.* in comparison with that of other small mammals) of the middle lobe of the cerebellum.

The lowermost part of this lobe is much more deeply cut off from the rest than it is in *Erinaceus* and *Perameles*. The simple folium so formed represents the "pyramis" of Human Anatomy. It is the dorsal lip of the fissura secunda, and the rest of the

middle lobe is much more deeply incised, *i. e.* has a much more extensive surface than that of all other mammals of a corresponding size.

Wherefore the cerebellum of *Tarsius* exhibits definite signs of superiority over that of other mammals when it is studied in mesial section.

The resemblance of the surface of the cerebellum in *Tarsius* to that of other small mammals is much closer than one might expect from a study of the mesial section.

The two lobules (nodule and uvula) of the posterior lobe extend outward for a short distance only and then seem—to the naked eye—to stop abruptly. If, however, a series of sections be examined microscopically, this lobe will be found to extend outwards as an exceedingly attenuated band of cortex which suddenly expands upon the lateral aspect of the middle peduncle of the cerebellum to form a short plump bilobulated mass—the flocculus.

The pyramid (which is the ventro-caudal lobule of the middle lobe) is prolonged outward into a broad band on the caudal aspect of the cerebellum. It arches outward and downward parallel to the margin of the uvula, so that it reaches the lower margin of the cerebellum. It then passes forward and expands, just above the flocculus, into a narrow, widely-projecting rod of cortex—the paraflocculus.

This paraflocculus is enclosed in a bony capsule formed by the petrous temporal. It is that part of the floccular lobe which is commonly called the “flocculus,” but it is not the flocculus of Human Anatomy.

The cortex on the upper side of the paraflocculus is divided into a series of five or six bands by means of shallow notches. The under surface is smooth. The distal extremity is bifid.

It is the distinctness of the broad cortical band joining the pyramid to the paraflocculus which specially emphasizes the resemblance of the cerebellum in *Tarsius* and that found in the generalized mammals. In most Primates this simple relationship becomes so completely disguised as to be quite unrecognizable.

For reasons which will appear later, it is desirable to have some term with which to distinguish the band of cortex linking the pyramid to the paraflocculus. I shall therefore call it the “copula pyramidis.” Exactly how much of the uniform band (in *Tarsius*) is pyramid and how much is copula, will be appreciated later when the different fate of the two parts will be studied.

The copula pyramidis forms the lowermost lobule of the lateral part of the middle lobe.

The rest of the latter is subdivided into three parts, which I distinguished by the letters A, B, and C in the Edentate cerebellum (*op. cit.*).

The area A is a simple band which forms the posterior lip of the fissura prima and extends outwards and forwards (on the anterior or cerebral surface) as far as the paraflocculus.

The area B is a little rounded knob which forms the most laterally-projecting part of the so-called “lateral lobe” of the cerebellum. It is subdivided into three folia by means of two deep fissures. The area B is wedged in between the lateral extremities of the areas A and C, and is connected to the mesial part of the middle lobe only by a very narrow stalk, the limiting furrows of which are always shallow and sometimes absent.

The area C is a little bifoliate nodule placed upon the caudal surface between the area B and the copula pyramidis which may be regarded as an area D. Unlike the area B, C is freely connected with the mesial parts by a broad band.

The fissures which indent the mesial part, so-called "vermis," of the middle lobe do not extend into the lateral regions. The limiting fissures of the areas A, B, C, and D arise laterally and do not extend on to the mesial area in *Tarsius*.

The anterior lobe differs in appearance from the other two lobes. It is broadest in the middle line and gradually tapers toward the region of the entrance of the middle peduncle into the cerebellum. Its surface is incised by two deep and three shallow fissures, the former of which extend as far as the middle peduncle.

In the brain of *Lemur*, the pattern exhibited in a mesial sagittal section of the cerebellum is much more complicated than that of *Tarsius*, but the plan is essentially the same (fig. 65). It so closely resembles that of *Orycteropus* which I have described in my memoir on the brain in the Edentata (*op. cit.* fig. 29, p. 362), that it is unnecessary to repeat the account. In the accompanying figure I have inserted letters to represent fissures homologous with those similarly distinguished in *Orycteropus*.

The general plan of the cerebellum closely conforms to the type found in such mammals as the Dog, the Anteater, and the smaller Apes.

The floccular lobe is divided, as in all mammals, into a ventral part—the flocculus—and a dorsal part—the paraflocculus. The flocculus consists of a little wedge-shaped mass closely applied to the lateral aspect of the pons Varolii immediately in front of the tuberculum acusticum and external to the trigeminal nerve. Its broad anterior aspect is subdivided into folia by five or six horizontal fissures. The posterior extremity of the wedge-shaped mass is connected by a long white band with the nodulus.

The paraflocculus consists of an irregular mass of folia placed on the dorso-lateral aspect of the flocculus, so that in a lateral view of the brain the latter is almost completely hidden by it. From its lowermost part (*i. e.* the region nearest the flocculus) a narrow stalk emerges and swells out into a plump projecting mass of folia arranged in a feather-like pattern. This projecting part of the paraflocculus is often called the "petrosal lobule" and more commonly simply "flocculus." It presents a similar form in all Apes except the Simiidae. In *Hylobates*, however, the typical Primate form of floccular lobe is fully developed.

The nearest approach to this type of floccular lobe among other mammals is exhibited in the Ungulata, of which the accompanying drawing of the lateral aspect of the Gazelle's cerebellum is typical (fig. 66).

In *Tarsius* the paraflocculus has been described as being directly linked by a simple cortical band to the pyramid. In *Lemur* a vastly different state of affairs obtains. Starting from the stalk of the so-called petrosal lobule, a series of folia (and not a continuous undivided band) forms a worm-like coil which curves forward, then upward and horizontally backward (compare the Gazelle's cerebellum, fig. 66). The series of disconnected folia then proceeds backward below the area B to the lower end of the area C, and it becomes impossible to accurately separate the series of folia belonging to the parafloccular (or perhaps it would be more accurate to say "copular") group



from those of the area C. The connection of the copula pyramidis with the pyramid becomes either entirely destroyed or reduced to exceedingly insignificant proportions. From comparative studies of the adult cerebellum it is quite impossible to decide the fate of the copula pyramidis in the larger cerebella. In many brains it seems to dwindle or completely disappear. In others again, especially *Simia satyrus*, it seems to undergo enormous expansion and form the greater part, if not the whole, of the body which is called tonsilla (amygdala) in Human Anatomy. This is a problem which can only be certainly settled by a study of its developmental history in a series of mammals.

The relations of these parts are considerably disturbed in the genera *Simia*, *Anthropopithecus*, and *Homo* by the extreme dwindling of the paraflocculus and the consequent disappearance of its "petrosal" part. The parafloccular remains become the flocculi secundarii of Henle.

Of the various subdivisions of the middle lobe of the cerebellum in *Lemur*, the area A is subject to perhaps the least change. It becomes furrowed by numerous new fissures, but they are approximately parallel to the fissura prima, and hence do not greatly disturb the pattern. The area A represents the lobus lunatus posterior, and is mesially continuous with the region between the fissura prima and the fissura b, which is called the clivus monticuli in Human Anatomy (fig. 65).

The area B is a very plump rounded mass which forms the lateral pole of the cerebellum (fig. 65). It consists of twelve vertical folia radiating in a feather-like pattern from a very narrow vertically-placed leaf-like stalk, the mesial part of which is deeply buried between the areas A and C. This stalk does not reach the mesial plane, for it becomes fused to the posterior aspect of the area A. The area B is the lobus postero-superior. There is no separate folium cacuminis.

The area C is a plump vertical worm-like band wedged in between the area B and the mesial parts of the middle and posterior lobes on the caudal surface of the cerebellum. Its connection with the suprapyramidal part of the "vermis" is constricted and depressed in a vertical furrow. In the Apes this vertical band rapidly increases in breadth, and the direction of its folia becomes oblique.

The general features of the anterior lobe are remarkably constant in all Mammals. The differences consist chiefly of an increase in the number of fissures in proportion to the size of the cerebellum.

In all other Prosimiæ the structure of the cerebellum does not vary to any marked extent from that of *Lemur*. In the smaller members the fissures become much fewer, and in *Microcebus* we find an organ which differs very slightly from that of *Tarsius*. In *Chiromys* the primitive connection between the pyramid and the paraflocculus, which has been seen to become obscured in *Lemur*, is retained in a distinct form.

[Since the foregoing pages were in type, some supplementary notes have been received from the author. In order not to delay the issue of this part, it is intended to publish the notes mentioned in an early number of the 'Journal' (Zoology), vol. 28.—Sec. Linn. Soc.]



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XI. *On the New Zealand Phyllobranchiate Crustacea-Macrura.*

By GEORGE M. THOMSON, F.L.S.

(Plates 27-29.)

Read 17th April, 1902.

THE proposed publication of a biographical census of the New Zealand Fauna makes it desirable to supervise many groups of animals, the members of which have been imperfectly described and in many cases incorrectly named. No groups have suffered more in this respect than the Crustacea, and, as a small contribution to our knowledge of this part of the fauna, I have lately been examining the Prawns and Shrimps of these islands, and find that very considerable revision is required in order to classify them correctly.

In Miers's 'Catalogue of the New Zealand Crustacea,' published in 1876, a summary of the then known species was given. Twelve species of Phyllobranchiate Macrura are there briefly described, but some of these are doubtful or incorrect. *Rhynchocinetes typus*, a species stated to be found also on the coasts of Australia and Chile, is introduced into the list of New Zealand species on the authority of British Museum specimens. Haswell also introduces it into the list of Australian Crustacea, apparently taking his description from Miers's Catalogue. No collector has, so far as I know, met with this species in this Colony, nor does it occur in any of the various local museums. I think, therefore, that its inclusion in our fauna is a mistake. I have recently received specimens of this very distinct and beautiful species from Mr. David G. Stead, of Sydney.

Again, Heller, in the Crustacea of the 'Novara' (p. 105), describes a Shrimp from Auckland, without any reference to its habitat, as *Caridina curvirostris*. This turns out to be the same as my *Leander fluvialis*; but both names are equally incorrect. The species is found only in fresh water, and belongs to the genus *Xiphocaris*.

The inclusion of *Atya pilipes* in the New Zealand fauna is due to an error, as first suggested by Miers himself, since the species is found in the Mid-Pacific islands, but not in New Zealand. Spence Bate ('Challenger' Report, p. 693) also states that *Atya armata* and *Atya spinipes* occur in New Zealand, but this is probably also an error.

Of the remaining species in Miers's Catalogue, *Alpheus novæ-zealandiæ* was described by him from specimens in the British Museum. This species does not appear to have been met with since, but this only emphasizes the fact that so few examples of the Crustacea occur in our local museums.

The 'Challenger' collections added twelve species, belonging to seven genera, to

the local fauna, but none of these are represented in our museums. They are all deep-sea species.

The following list includes the names of all the species known up to the present time.

### Tribe CRANGONIDEA.

#### Family CRANGONIDÆ.

##### Genus 1. PONTOPHILUS, Leach, 1817.

##### 1. PONTOPHILUS AUSTRALIS, G. M. Thomson. (Plate 27. figs. 1-5.)

1879. *Crangon australis*, Hutton, MS.; G. M. Thomson, Trans. N.Z. Inst. vol. xi. p. 231, pl. 10. fig. A 1.

Carapace (fig. 1) about one-third of the length of the animal, the whole surface somewhat rugose with very short hairs, and bearing five irregular longitudinal rows of spines. The rostrum is very short, blunt, and hollowed above, and does not extend beyond the eye-stalks. The eye-sockets are semicircular, their lower limit defined by a sharp spine. The margin then inclines a little forward, and at its lower edge ends in a rather long acute spine; the whole margin is rather setose. On the median line the carapace is slightly ridged and carries two short spines; on each side and behind the orbital spine is a second row of four spines; and on the lower lobe of the carapace are two acute spines, the posterior one at a little distance from the margin. The pleon is nearly smooth. Its second segment is shorter on the dorsal line than the first, but its lower margins are produced both backwards and forwards into rounded broad lobes. The third and fourth are subequal in length; the lateral margins of the fifth are produced posteriorly into a two-spined lobe. The sixth segment is two-ridged above, and ends on the sides in a three-spined process. The telson reaches to the extremity of the tail-fan; it is narrow and tapering, its margins are fringed with setæ, and it ends in three minute teeth and a number of plumose hairs.

The eye-stalks are short, stout, and blunt; the eyes are reniform.

The first antennæ (fig. 2) have the broad plate on the outside of their base reaching nearly to the extremity of the first joint; the latter is produced on its outer distal margin; the second and third joints diminish in length; the flagella are short.

The second antennæ have the scaphocerite about twice as long as broad, produced considerably beyond the peduncle, and ending in a strong tooth.

The third maxillipeds are much elongated, extending considerably beyond the plate of the first antennæ. According to Spence Bate ('Challenger' Macrura, p. 482), the dactylos and propodos are wanting in the members of this family; while Stebbing (South African Crust. p. 47) says: "in the third maxillipeds it is clear that the geniculation occurs between the fourth and fifth joints, and in all probability the sixth, which is much longer than the fifth, represents a coalescence of the sixth and seventh joints." In this

species (fig. 3) the basal joint bears a short appendage (basecphysis) not reaching to the extremity of the meros. The ischium is very short and almost completely merged into the next joint, the meros. The carpus is about half as long; while the terminal joint is again elongated, bearing a few spines on the lower margin among the numerous hairs, and ending in two very short spines.

The first pair of pereiopoda have the meros (fig. 4) keeled on the upper margin and produced into an acute spine, the lower margin being flattened and winged to partially receive the hand when bent inwards. The hand is about three times as long as broad, and its inferior margin ends in a straight spine; the palm is very oblique.

The second pair of pereiopoda are very short and feeble, only about half as long as the succeeding pair; both fingers of the slender chelæ are subequal and fringed with hairs.

The third pair are long, very slender, and stiliform, and extend beyond the extremity of the flagella of the first antennæ.

The fourth and fifth pairs are strong, with long and acute dactyla.

The posterior pair of pleopoda (fig. 5) are subequal with the telson; the outer branch has the outer margin terminating in a short subapical tooth; the inner is narrower and rather longer.

The colour is a uniform sandy grey; occasionally the fifth segment of the pleon is coloured dark brown or has patches of brown coloration on it.

The following are the dimensions of a large ovigerous female:—

	mm.
Extreme length . . . . .	38
Breadth at second segment of carapace . . . . .	7
Length of carapace . . . . .	12
„ scaphocerite of first antennæ . . . . .	6
„ last segment of pleon . . . . .	5
„ telson . . . . .	7

*Habitat.* This is a common species on the New Zealand coasts within the 20-fathom line, as the following list of localities shows:—Dusky Sound, Paterson Inlet (Stewart Island), Otago Harbour, Blueskin Bay, Akaroa, Lyttelton Harbour, and Cook Strait. Also at Napier (*Filhol*).

*Distribution.* Confined to New Zealand.

## 2. PONTOPHILUS GRACILIS, Bate.

1888. Bate, 'Challenger' Macrura, p. 487, pl. 87.

*Habitat.* Off the New Zealand coast, east of Cape Turnagain, in 1100 fathoms.

*Distribution.* Off Tristan da Cunha, near Torres Straits, and near the Philippine Islands.

## Tribe POLYCARPIDEA.

## Family PROCESSIDÆ.

## Genus 1. GLYPHOCRANGON, A. Milne-Edwards, 1884.

## 1. GLYPHOCRANGON REGALIS, Bate.

1888. Bate, 'Challenger' Macrura, p. 517, pl. 93. figs. 3 & 4.

*Habitat.* North of the Kermadec Islands, 600 fathoms.

*Distribution.* Off Fiji and Banda Islands, at depths of 200 and 315 fathoms.

## Family ALPHEIDÆ.

## Genus 1. ALPHEUS, Fabricius, 1798.

## 1. ALPHEUS SOCIALIS (Heller). (Plate 27. figs. 6-12.)

1865. Heller, Voy. 'Novara,' Crust. p. 106, pl. 10. fig. 1.

1876. Miers, Cat. N.Z. Crust. p. 82.

The carapace is produced into a very short acute rostrum, the lower margin of which is straight; over each orbit it is produced into a rounded lobe which ends in a minute spine; the posterior margin is straight on the dorsal portion, but on the sides is slightly produced backwards; in length it is barely one-third as long as the body.

The first antennæ have the basal scale about as long as the first joint of the peduncle; it is broad and flat above, and the basal portion of its outer margin is finely serrated; the second joint of the peduncle is twice as long as the first. The outer flagellum is stouter than, but less than half the length of, the inner (which is about two-thirds as long as the animal), and tends to divide into two at the apex.

The second antennæ have the basal scale reaching to the extremity of the peduncle of the first pair; the basal spine is about half as long and very acute; the flagellum nearly as long as the body.

The first pereopoda are very unequal, the left being the largest in all my specimens. In the largest specimens the propodos of the left limb has the upper and lower margins nearly parallel, the upper having a narrow groove or channel, while the lower is transversely rugose; the dactylos is strongly curved and bent outwardly, while on the inner side it is furnished with a stout blunt tooth. In smaller ovigerous specimens the dactylos is rounded and less claw-like, as if it had lost its chelate function (fig. 9). At the hinge of the dactylos and propodos the opposing surfaces are flat and circular. In the right limb the dactylos is about half as long as the propodos, is well developed, and slightly curved; the inner faces of the claw are densely fringed with hairs.

The second pereopoda are considerably longer than the succeeding pair. The three

following pairs have the propoda (fig. 10) furnished with numerous spines on the lower margin, and the dactyla with a strong inner tooth.

The last pair of pleopoda have the inner branch evenly rounded; the outer (fig. 12) crossed near the extremity by a strong diæresis, the outer margin of which carries a strong spine.

The telson (fig. 11) bears two spines on its upper surface near each margin; its truncate and slightly rounded apex is about half as wide as the base, and ends in a fringe of setæ.

The following are the dimensions of a large male:—

	mm.
*Entire length . . . . .	48
Length of carapace . . . . .	15
Depth of carapace . . . . .	10
Length of pleon . . . . .	24
„ 1st pereopod (left) . . . . .	37
„ propodos of same . . . . .	22
„ dactylos of same . . . . .	8
„ 1st pereopod (right) . . . . .	34
„ propodos of same . . . . .	18
„ dactylos . . . . .	10
„ telson . . . . .	9

*Habitat.* This species occurs fairly commonly in the North Island, and as far south as Cook Strait and Tasman Bay. I have specimens from the following localities:—Waiwera, Auckland, Hauraki Gulf (*L. F. Ayson*), Moko Hinau (*Sandager*), Portland Island (*Robson*), Wellington Harbour (*Farquhar*), and Tasman Bay, Nelson. I have never obtained any specimens from the east coast of the South Island, the waters of this part being more or less cooled by an Antarctic current, and *Alpheus* being apparently a genus which loves the warmer seas.

*Distribution.* Australia.

Mature specimens sent me from Port Phillip by Mr. S. W. Fulton, and which are not more than an inch (25 mm.) long, agree in nearly all details with the above, only the large left hand is like those of my smaller specimens in having the rounded dactylos, the supraorbital spines are much more produced (fig. 8), and the extremity of the telson is somewhat more rounded.

In the 'Challenger' *Macrura* (p. 540), Spence Bate gives a list of species of *Alpheus*, and refers *A. socialis* to Australia, and *A. chiragricus*, M.-Edw., and *A. noræ-zealandiæ*, Miers, to New Zealand. According to M.-Edwards (Hist. Nat. Crust. vol. ii. p. 354), *A. chiragricus* occurs in the seas of Asia, and I have seen no subsequent reference to its occurrence in New Zealand. From the brief description given by M.-Edwards it is a distinct enough species.

\* In all the rostrum-bearing species, I have measured the length from the point of the rostrum to the apex of the telson.

2. *ALPHEUS* NOVÆ-ZEALANDIÆ, Miers.

1876. Miers, Ann. & Mag. Nat. Hist. ser. 4, xvii. p. 224; Cat. N.Z. Crust. p. 82, pl. 2. fig. 2.

I do not know this species. Miers says it "is distinguished by the absence of spinules on the upper orbital margin, the shorter basal spine of the external antennæ, &c.,"—characters almost too indeterminate to found a specific distinction upon.

Genus 2. *BETEUS*, Dana, 1852.

It is difficult to find a definite character on which to base the generic distinction between *Betæus* and *Alpheus*. The two points emphasized by Dana are the absence of a rostrum and the inverted position of the propodos of the first pereiopods. But Stimpson gives as the principal character of the Australian *B. trispinosus*, "front with a long needle-like rostrum, and armed with two acute orbital teeth, which are half the length of the rostrum." In our New Zealand species these orbital teeth are present, though small, and are not on the margin of the carapace, but on the front of the eyes. The twisting of the first pereiopods, by which the dactylos is on the lower side of the propodos, appears to me to be due to a slight twisting of all three joints—the meros, carpos, and especially the propodos.

The ova, as pointed out by Spence Bate (Chall. Macr. p. 564), are much larger and more oval than the small spherical ova of *Alpheus*. The only New Zealand species appears to be very distinct. Spence Bate, considering a mutilated specimen of an Australian species, *B. microstylus*, was inclined to assign it to *B. æquimanus*, but his figures are conclusive against this identification.

1. *BETEUS* *ÆQUIMANUS*, Dana. (Plate 28. figs. 1, 2.)

1852. Dana, U.S. Explor. Exped. xiii., Crust. part i. p. 560, pl. 35. fig. 11.

1876. Miers, Cat. N.Z. Crust. p. 83.

The front of the carapace is notched about as deep as the eye-sockets (fig. 1), above which it rises slightly, and is again slightly notched beneath them; its antero-inferior angle is rounded. The posterior margin is somewhat convex and acutely notched on each side of the dorsal surface, the postero-lateral portions being produced backwards into a rounded lobe which lies *under* the first segment of the pleon.

The second segment of the pleon has the sides greatly produced both forwards and backwards.

The telson (fig. 2) is wedge-shaped, its apex ending in a blunt tooth on each side, with a somewhat rounded portion between, bearing a row of plumose setæ.

The ophthalmopods are short, depressed, and slightly projecting from under the front of the carapace; the eyes are nearly circular, and occupy the greater portion of their upper surface. In front they are produced into a small spinule.

The first antennæ have the joints of the peduncle subequal in length and diameter, the first being slightly the longest. The basal scale reaches to the extremity of the second joint. The outer short flagellum shows the normal tendency to divide into two at the apex.



The second antennæ have the peduncle only slightly exceeding that of the first pair. The basal joint is produced into a short triangular lobe on the lower margin; the scaphocerite reaches nearly to the end of the peduncle, and its outer spine is short. The flagella are thick and tapering, and though I have not been able to observe the movement, I am inclined to think they help the animal to spring.

The third maxillipeds are slender, and do not reach to the extremity of the peduncle of the first antennæ.

The first pereopoda are not very strongly developed and are subequal in form; the triangular carpos is produced on its lower side into a rounded lobe; the propodos is about as long as the rest of the limb and slightly curved at its extremity; the dactylos is short and curved, and, as well as the opposed pollex, is somewhat hairy at the tip.

The second pereopoda are normally long and slender; the carpos is 5-jointed, the three middle joints being together equal to the first and last in length.

The succeeding pereopoda are very strong and stout, and are used for walking over the rocks and among the weed in which this species is found; the third pair are the strongest.

The pleopoda have short, broad, foliaceous branches, except the first pair, which have one of the branches long and slender, and the other rudimentary.

The last pair, forming the tail-fan, are nearly twice as long as the telson, and the plates are broad and spreading; the outer is divided by a distinct diæresis into two nearly equal parts, the upper margin ending in a strong spine; the inner is ovate in form, and ends in two strong spines.

The integument is somewhat rough with harsh points, especially on the limbs, and these are rather hard and brittle, as is so often the case with shore species.

The colour appears to be dependent on the surroundings. The specimens from Stewart Island, taken under stones, were of a uniform brownish-red colour; those from Moeraki, caught on the seaweed, were olive-green.

The normal mode of progression appears to be by walking, but when disturbed the animal escapes by vigorous leaps of a foot or more in length.

The following are the dimensions of a large male:—

	mm.
Entire length . . . . .	30
Length of carapace . . . . .	10
„ telson . . . . .	3
Depth of carapace . . . . .	5.5
Length of 1st pereopod . . . . .	10
„ 1st antennæ to end of flagellum . . . . .	11

*Habitat.* This species occurs most commonly under stones or among weed between tide-marks, less rarely in rock-pools. It is probably common on the coast. I have it from the Bay of Islands (where Dana's original specimens were collected), Waiwera, Cape Campbell, Moeraki, Dunedin Harbour, Stewart Island, and Chatham Islands (*H. B. Kirk*). Filhol records it from Cook Strait.

*Distribution.* Confined to New Zealand.

## Family HIPPOLYTIDÆ.

## Genus 1. ALOPE, White, 1847.

1847. White, Proc. Zool. Soc. p. 123.

1848. White, Ann. & Mag. Nat. Hist. ser. 2, vol. i. p. 225.

1876. Miers, Cat. N.Z. Crust. p. 84.

Carapace smooth, with a supraorbital spine and a suborbital tooth on each side. Rostrum short, armed with teeth above, and springing from a deep groove.

Ophthalmopoda short, stout; ocellus well developed.

First antennæ short, with two flagella.

Second antennæ with a large scaphocerite and a very long flagellum.

Mandible with shortened cutting-tooth (psalistoma) and a three-jointed palp (synhipod).

First maxillæ 2-branched; second pair 3-branched, with wide mastigobranchial plate.

First maxillipeds with a 2-lobed mastigobranchia.

Second maxillipeds with a short podobranchial plume.

Third maxillipeds very long and pediform, without any trace of branchiæ.

First pereopoda strong; chelæ well developed.

Second pereopoda very slender, long, and minutely chelate; carpos 7-articulate (or 9-articulate)\*.

Third to fifth pereopoda slender, with bifid dactylos.

Telson long and narrow.

The branchial formula is as follows:—

	<i>h</i>	<i>i</i>	<i>k</i>	<i>l</i>	<i>m</i>	<i>n</i>	<i>o</i>
Pleurobranchiæ . . . .	—	—	1	1	1	1	1
Podobranchia . . . . .	1	—	—	—	—	—	—
Mastigobranchiæ . . . .	—	r	r	r	r	r	r

The mastigobranchiæ are extremely rudimentary, consisting of a minute tubercle with a mere trace of a plume.

Miers placed this genus in the Alpheidæ, but its distinct rostrum, exposed ophthalmopods, mandibles with reduced psalistoma, the symmetrical first pereopods, and narrow tapering telson lead me to include it among the Hippolytidæ.

## 1. ALOPE PALPALIS, White. (Plate 28. figs. 3-12.)

1847. White, *l. c.*, &c.

1874. Miers, Zool. 'Erebus' & 'Terror,' Crust. p. 4, pl. 4. fig. 1.

The carapace is broad, widening posteriorly; in front it bears a 4-toothed slender rostrum, two teeth being near the point of origin, and two on the distal portion; the lower margin is entire. On each side of the rostrum, and about half its length, stands a

\* See specific description, p. 441.

strong acute spine. Below the orbit the front margin is produced into a short tooth. The posterior margin of the carapace is rather deeply hollowed dorsally; the sides are deep.

The pleon is about twice as long as the carapace; its second segment is not very much produced on the sides.

The telson is long and tapering, with a deep groove along the centre; its extremity bears two long spines, with a short one at each side (fig. 4).

The first antennæ (fig. 5) have the basal joint broad and produced on the outer side into a spine which reaches to the middle of the second joint; the inner side bears a small tubercle near its base; the apex of the joint bears a transverse comb of small spinules both above and below. The second and third joints together barely equal the first in length, and the latter bears a very short joint on its outer side, from which springs the short thick flagellum, the inner flagellum being long and slender.

The second antennæ have the peduncle slightly exceeding in length the peduncle of the upper pair. The scaphocerite is long and rather narrow, and is produced into a spine on its outer margin, which is subequal with the peduncle in length. The flagellum is longer than the whole body of the animal.

The mandibles (fig. 6) have a cylindrical molar process, a short and much-reduced cutting-tooth (psalistoma), and a 3-jointed palp (synhipod).

The first maxillæ (fig. 7) are two-branched, the larger (outer) branch consisting of an obovate plate fringed with setæ.

The second maxilla (fig. 8) is three-branched; the inner branch small, very short, and broad; the second long and plate-like, bifid, and fringed with setæ; the third slender and stiliform; mastigobranchial plate wide, produced both back and front.

The first maxilliped (fig. 9) bears a bilobed mastigobranchial plate, a flat broad basal plate fringed with setæ, a long cylindrical branch, and on the inner side of the latter a smaller more slender branch (cephysis?).

The second maxillipeds (first gnathopoda of Spence Bate) (fig. 10) have a short broad plate on the inner face of the coxa, and on its outer a short branchial plume; the basos carries a long cylindrical branch fringed towards the extremity with setæ; the ischium and meros are short, broad, and curving round; the carpos is broader than long, and bears a very broad but short propodos fringed with hairs.

The third maxillipeds are long and pediform; the basal joint is furnished with a slender single-jointed branch, and there is no trace of branchiæ on the limb.

The first pereopoda are well developed, and are rough on their outer surface and edges with small spinules; the long triangular meros and the short carpos (which latter ends above, or rather on the outer side, in two or three strong teeth) have deep sockets at their extremities to receive the base of the succeeding joint.

The second pereopoda (fig. 11) are long and slender; the basos is very short, the ischium long and divided into two unequal joints, the meros still longer, and also divided into two joints, the carpos seven-jointed, and the propodos short, with a minute chelate dactylos.

The relative value of the joints of this limb is rather difficult to estimate. If we count

the first four joints as normal, and then regard all those between the fourth and the propodos as forming the carpos, then the latter is nine-jointed. But a glance at the limb itself seems to suggest that this is a forced and not very natural mode of treating it. The normal mode of folding the limb into three parts takes place at what I have assumed to be the distal ends of the ischium and meros respectively. On the other assumption I should describe the ischium and meros as straight, the latter about half as long as the former, the carpos as nine-jointed, first joint about as long as the two preceding, second half as long, remaining seven usually bent at a considerable angle and not quite so long as the first two.

The third to the fifth pereopoda are well developed and diminish in size posteriorly. The dactyla (fig. 12) are strongly toothed below so as to be two-clawed.

A small tubercle projects from the sternum between the bases of the third pereopoda, and a larger keeled protuberance between the bases of the fourth pair. This latter sternal segment is produced posteriorly into two small acute lobes (fig. 3).

The first pleopoda in the males have a stout basal joint longitudinally folded at right angles; the two foliaceous plates are slender and acute, and the outer projects outwardly nearly at right angles to the inner, so as to stick out from the sides of the animal like two minute fans.

The succeeding three pairs of pleopoda have the basal joints rather long and stout, and the foliaceous plates subequal with them in length. The fifth pair are shorter and thicker.

The sixth pair have the foliaceous plates subequal, narrow and rounded at the end, and somewhat exceeding the telson in length.

The dimensions of a male specimen were:—

	mm.
Entire length . . . . .	77
Length of carapace to extremity of rostrum . . . . .	25
Depth of carapace . . . . .	14
Length of rostrum from first dorsal tooth . . . . .	11
„ pleon . . . . .	52
„ telson . . . . .	12
„ first antennæ . . . . .	28
„ second antennæ . . . . .	85
„ peduncle of same . . . . .	12
„ external maxillipeds . . . . .	54
„ first pereopoda . . . . .	33
„ second pereopoda . . . . .	37

*Habitat.* I have only met with this species in rock-pools from the following localities.—Cape Campbell, Sumner, Moeraki, Otago Heads, and Stewart Island. Filhol also records it from Cook Straits.

*Distribution.* Australia.

Genus 2. HIPPOLYTE, Leach, 1815.

The generic character, as limited by Spence Bate, is given at length in the 'Challenger' Macrura, p. 587.

1. HIPPOLYTE BIFIDIROSTRIS, Miers. (Plate 28. figs. 13-16.)

1876. *Virbius bifidirostris*, Miers, Ann. & Mag. Nat. Hist. ser. 4, xvii. p. 224; Cat. N.Z. Crust. p. 81, pl. 11. fig. 1.

Carapace with a prominent acute spine over the eye-socket, a second subocular spinule on the front margin just between the bases of the two pairs of antennæ, and a third just close to the margin behind the base of the second antenna; infero-anterior angle subacute. Rostrum subequal with or slightly longer than the carapace; upper margin with two teeth placed just above the eyes, and a minute notch at the apex; lower margin with five to seven teeth.

The pleon is sharply bent (in all spirit-specimens) at the extremity of the third segment, the dorsal margin of which is slightly produced and hood-like. The fourth and fifth segments have their inferior margins produced considerably back into rounded and subacute lobes respectively.

The telson is long, narrow, and slender, ending at its slightly rounded apex in a row of small spinules.

The ophthalmopods (fig. 13) are rather elongated, and scarcely dilated towards the extremity; the eyes only occupy about a third of their length.

The first antennæ (fig. 14) have the first joint of the peduncle flattened, and broadened on the inside into a narrow wing which ends in a spine; the basal scale is acute and nearly as long as the first joint of the peduncle. The outer flagellum is short and imperfectly segmented, as seems to be usual in species of this genus.

The second antennæ have the peduncle very short, and the scaphocerite oval and reaching beyond the extremity of the rostrum; the flagellum is very slender and often as long as the entire animal.

The third maxillipeds (fig. 15) are long and stout; the third joint is subequal in length to the fourth and fifth together; the latter terminates in a number of minute spines.

The first pereopoda (fig. 16) are very short and stout; the carpos is produced on its upper margin into a blunt spine; the propodos is subquadrate in form.

The second pereopoda are nearly twice as long as the first pair; the ischium, meros, and carpos are about subequal in length, the latter being three-jointed and having the middle joint the shortest; the propodos is short and straight, with a stout straight dactylos.

The succeeding pairs of pereopoda are long and well developed; the propoda have a few long spinules on their lower margins, while the long straight dactyla are pectinately spined.

The pleopoda are well developed, and the inner branches of the females bear a well-developed process (stylamblys of Spence Bate).

The sixth pair are narrow and rather longer than the telson; the outer one with a two-spined outer margin and a well-developed diæresis.

The dimensions of a mature female were:—

	mm.
Entire length . . . . .	41
Length of carapace . . . . .	14
„ rostrum . . . . .	7
„ sixth segment of pleon . . . . .	4
„ telson . . . . .	6
„ first antennæ . . . . .	28
„ first pereopoda . . . . .	5
„ second pereopoda . . . . .	7

*Colour.* Specimens taken in the trawl outside Otago Harbour were bright green when alive.

*Habitat.* Kenepuru (*J. McMahon*), Otago Heads, 20 fathoms (trawled); Paterson Inlet, Stewart Island, 10 fathoms (dredged).

*Distribution.* Confined to New Zealand.

### Genus 3. MERHIPPOLYTE, Bate, 1888.

‘Challenger’ Macrura, p. 618.

#### 1. MERHIPPOLYTE SPINIFRONS, M.-Edwards.

1837. *Hippolyte spinifrons*, M.-Edw. Hist. Nat. Crust. ii. p. 377.

1843. *Hippolyte spinifrons*, White, Dieff. N. Z. ii. p. 268.

1875. *Hippolyte spinifrons*, Miers, Cat. N.Z. Crust. p. 80.

1885. *Hippolyte spinifrons*, Filhol, Miss. de l'Île Campbell, p. 431, pl. 53.

The following is the description given by Filhol (*l. c.* p. 431):—“The smooth carapace bears on its anterior and median portion a very strong spine (rostrum), which reaches beyond the front of the eyes. This spine has on the anterior portion of the upper margin two acute teeth directed forwards. Two much smaller spines are produced on the median line immediately behind the first one. These are reduced and are directed upwards and forwards. Immediately outside of the frontal anterior spine are two other long spines without teeth, which project as far as the space between the two little teeth on the rostrum. The ocular peduncle is completely hidden. The first antennæ have the basal joint rather large, and they bear two flagella, the one long and slender, the other short and strong, and about half as long as the preceding one. The second antennæ have only one flagellum; the outer portion of the upper margin of the basal joint is two-toothed; the palp is moderately enlarged. The first two pairs of feet are slightly developed and of equal length; each of them ends in a small didactyle hand. The second pair is shorter than the third, and its carpos is multiarticulate; it ends in a very small didactyle hand. The third pair of feet is the strongest. The upper margin of the third joint of the last three pairs of feet ends in a small spine; the extremity of the fingers bears on its inferior

margin three or four little tufts of hairs. The third maxillipeds are long, pediform, and rather large; the terminal joint ends in an acute apex. The length from the apex of the frontal spine to the extremity of the telson is 37 mm. The telson is remarkable on account of the triangular form of its apex; it bears three pairs of small spines, of which one is very much reduced and scarcely visible.

"This species, which I collected at low water in the rock-pools, appears to me to be rather abundant. It occurs, without any indication of its habitat in New Zealand, in the collections of the Museum of Paris. The development of the suborbital spines enables it to be recognized at the first glance."

*Habitat.* Lyall's Bay, Wellington (*Filhol*).

*Distribution.* Confined to New Zealand.

I have not met with this species.

Spence Bate suggests that *M. orientalis*, one of the 'Challenger' species described by him, and which was taken off New Guinea in 690 fathoms, is the same species.

#### Genus 4. NAUTICARIS, Bate, 1888.

'Challenger' Macrura, p. 602.

##### 1. NAUTICARIS STEWARTI, G. M. Thomson. (Plate 29. fig. 1.)

1888. *Hippolyte Stewarti*, G. M. Thomson, Trans. N.Z. Inst. xvi, p. 259, pl. 13. fig. 1.

Carapace relatively deep, depth nearly equal to half its length; surface smooth; subocular spine well developed; infero-anterior margin produced into a small spine. Rostrum very acute, about as long as the rest of the carapace; upper margin with six prominent teeth, lower produced deeply and with two acute teeth.

Pleon with the third to the fifth segments produced backwards on their lower margins into acute teeth; sixth segment also produced back into an acute tooth on either side above the lower margin, which bears the characteristic movable spine.

Telson narrow-oval; apex rounded, bearing two spines and a number of slender setæ.

Ophthalmopods short and thick; eyes occupying the slightly dilated upper half.

First antennæ have the basal joint longer than the next two together; stylocerite reaching to extremity of the second joint; inner flagellum not much longer than the peduncle, considerably stouter than the outer.

Second antennæ with a slender peduncle, equalling that of the first pair in length; flagellum ? (missing); scaphocerite twice as long as the peduncle, very narrow and tapering, the spine reaching beyond the foliaceous plate.

The mandibles, maxillæ, and maxillipeds closely resemble the same organs in *N. marionis* as figured by Spence Bate ('Challenger' Macrura, pl. 108).

The pereopoda are similar to those of *N. marionis*. In the second pair the carpos is 14-15-jointed. In the succeeding pairs the claws are all didactyle.



The following are the dimensions of the only specimen :—

	mm.
Length of entire animal . . . . .	28
„ carapace . . . . .	10
„ rostrum . . . . .	5
„ pleon . . . . .	15
„ third segment of pleon . . . . .	2.5
„ sixth „ „ . . . . .	2
„ telson . . . . .	3

*Habitat.* A solitary specimen was taken by the dredge in Paterson Inlet, Stewart Island, in 10 fathoms.

*Distribution.* Confined to New Zealand.

This species is so near *N. marionis*, Bate, that I retain it with some hesitation. It differs markedly in the dentition of the rostrum; and although this is a very conspicuous character, yet I am inclined to think that it is a variable feature, and consequently of little value as a specific distinction. Bate describes the telson as bearing three pairs of spinules, rather an unusual feature in the family. My specimen has only the usual two.

The 'Challenger' specimens of *N. marionis* were taken off Marion Island in 69 fathoms, and Prince Edward Island in 140 fathoms, both localities nearly due south of Africa, and off the Falkland Islands in South America in 12 fathoms.

#### Family PANDALIDÆ.

##### Genus 1. PLESIONIKA, Bate, 1888.

###### 1. PLESIONIKA SEMILEVIS, Bate.

1888. Bate, 'Challenger' Macrura, p. 644, pl. 113. fig. 3.

*Habitat.* Off the Kermadec Islands, 520 fathoms.

*Distribution.* Philippine Islands, Borneo, Fiji, and east coast of Australia, from 250 to 1200 fathoms.

##### Genus 2. PANDALUS, Leach, 1817.

###### 1. PANDALUS MAGNOCULUS, Bate.

1888. Bate, 'Challenger' Macrura, p. 667, pl. 115. fig. 1.

*Habitat.* Stations 166 and 167 in Tasman Sea, west of New Zealand.

*Distribution.* Confined to New Zealand.

## Tribe MONOCARPIDÆ.

## Family ATYIDÆ.

## Genus 1. XIPHOCARIS, von Martens, 1872.

*Xiphocaris*, von Martens, Arch. f. Naturg. xxxviii. pt. 1, p. 139 (1872).

"Rostrum slender, compressed, dentate, usually long. All the pereopoda slender and with exopodites; carpal joints of first two pairs without a distal excavation, articulating in a normal way with the proximal end of the propodus. Abdomen with sixth segment elongate; telson slender, truncate at tip." (*Mary J. Rathbun*, 'The Brachyura and Macrura of Porto Rico,' p. 118.)

## 1. XIPHOCARIS CURVITROSTRIS (Heller), G. M. Thomson. (Plate 29. figs. 2-13.)

1865. *Caridina curvirostris*, Heller, Voy. Novara, Crust. p. 105.

1876. *Caridina curvirostris*, Miers, Cat. N.Z. Crust. p. 78.

1879. *Leander fluvialilis*, G. M. Thomson, Trans. N.Z. Inst. vol. xi. p. 231, pl. 10. fig. A 2.

Carapace nearly twice as long as deep, the lower margin curved in towards the body; front furnished with a prominent spine above and another below the eye-socket. Rostrum slender and slightly curved upwards, 11-12-toothed above, beginning as a slight crest on the carapace, with two or three teeth behind the eyes, a central group of four or five in front of the eyes, and three or four small teeth close to the apex; 4-6-toothed below.

Pleon having the second segment greatly dilated in the females, extending forward over the posterior margin of the carapace; fourth and fifth segments with their infero-posterior margins produced back into angular projections, which are more or less fringed with setæ. Sixth segment nearly as long as the fourth and fifth together.

Telson (fig. 3) rather long, narrow, and slightly tapering; on each margin it bears two short spines on its distal half. The extremity is slightly rounded and ends in two very short marginal spines and about six slender short setæ.

The ophthalmopoda are nearly pyriform, the upper half being occupied by the large rounded eye; the peduncle has a minute rounded lobe just at its base on the inner side.

The first antennæ (fig. 4) have the peduncle reaching almost as far as the extremity of the rostrum. The first joint reaches beyond the ophthalmopod, and from the base of its outer margin there projects forward a stout stylocerite, which reaches halfway along the next joint; its outer margin is also somewhat produced. The second joint is shorter than the first, while the third is only about half as long as the second. The flagella are both rather slender, the outer being imperfectly divided into two.

The second antennæ (fig. 5) have a slender peduncle reaching only to the middle of the second joint of that of the first pair; the second joint is produced on its outer margin into a short spine. The scaphocerite is produced along its outer margin into a spine which reaches the extremity of the peduncle of the first antennæ, while the oval-pointed

foliaceous plate is produced considerably beyond it; the flagellum is slender and nearly as long as the body of the animal.

The mandibles (fig. 6) have a very distinct curved molar process and a well-developed four-toothed cutting-plate; there is no palp present.

The first maxillæ (fig. 7) are small, feeble, and three-branched; the outer branch is short, ovate, and bears two fine terminal setæ; the middle one is the largest and broadens distally, its edge being fringed with short spines; the inner is short and has a rounded finely setose edge.

The second maxillæ (fig. 8) consist of two distinct processes: an inner formed by two broad, straight-edged, overlapping plates with a thick fringe of setæ on their edges, and overlapped at their base by two smaller, rounded, fringed plates; the outer process extends forward into a slender, rounded, fringed plate, and backward into a long slender portion ending in long setæ, which lie in the branchial cavity of the body. Between the two main portions of the limb there is produced a very small, slender, and rudimentary one-jointed process, only visible under the microscope.

The first maxillipeds (fig. 9) are two-lobed, the inner lobe being semicircular and fringed on the straight inner edge with numerous setæ, the outer shorter and thinner; between them, and apparently projecting from the basal joint, is a long, slender, slightly flattened process.

The second maxillipeds (fig. 10) have a short podobranchia on the coxal joint, and a long plumose branch (ecphysis) on the basos; the ischium is short, the meros still shorter, while the carpos is dilated into a short fringed plate; the propodos is bent against the preceding joints in the form of a large fringed plate. I can find no trace of a dactylos.

The third maxillipeds (fig. 11) are long and pediform, four-jointed; the short basal joint carries a long exopodite; the next three are long and subequal, the terminal one bearing numerous spines.

The first pereiopoda (fig. 12) are comparatively short and stout; the exopodite reaches nearly to the propodos; the carpos is short, broadened at its deeply excavated apex; the stout propodos articulates with it at its lower angle; the dactylos and pollex are thick, spoon-excavate on their inner faces, and furnished with a thick tuft of hairs at their extremities.

The second pereiopoda (fig. 13) are considerably longer and more slender than the first pair; the exopodite reaches only to the extremity of the meros; the carpos is long, excavate at the tip, and the propodos, which resembles that of the first pair but is more slender, is also attached to it by its lower angle.

The three posterior pairs are long and nearly unarmed, except for a few spinules on the meros and propodos; the dactyla are simple; each limb bears a well-developed exopodite.

The pleopoda have strongly developed foliaceous plates, and each bears a stylamblys. The sixth pair have the basal joint short, and produced on the outer margin into a tooth; the foliaceous plates are subequal in length, and the outer is crossed by a well-defined diæresis.

The following are the dimensions of a mature female:—

	mm.
Length of entire animal . . . . .	39
„ carapace . . . . .	9
„ rostrum . . . . .	8
„ pleon . . . . .	22
„ second segment of pleon . . . . .	5
„ sixth „ „ . . . . .	5
„ telson . . . . .	6

*Habitat.* Freshwater streams apparently throughout the Colony. I have it from the neighbourhood of Dunedin, Christchurch, Nelson, and Greymouth, also from the Buller River in the South Island; and from the Waikato and the neighbourhood of Auckland in the North Island.

*Distribution.* Confined to New Zealand.

This species is distinct from the Australian *X. compressa*, the most conspicuous difference being in the number of spines on the rostrum. While *X. curvirostris* shows only slight variation in this respect, the Australian form is rather variable. Ortmann (Proc. Acad. Philadelphia, 1894, p. 400) states that it has from 20 to 24 teeth on the upper, and from 2 to 4 on the lower margin. But the following figures give the dentition of a number of specimens from different localities, the first figure representing the number of teeth on the upper, and the second the number on the lower margin:—

From Victoria.—(1) 26—2; (2) 14—5, this one had the end broken.

From N. S. Wales.—(1) 31—9; (2) 23—7; (3) 24—6; (4) 24—5; (5) 26—4.

From Norfolk Island.—(1) 31—5; (2) 27—9; (3) 34—7; (4) 25—6; (5) 22—7.

From Norfolk Island.—(1) 22—3; (2) 21—2; (3) 17—3.

The last three belonged to a form smaller than those previously received from Norfolk Island, and having a shorter rostrum. From the above it appears that the dentition of *X. compressa* may be expressed as follows:—Upper margin with 17–34 teeth; lower with 2–9.

It is interesting to notice that while one slightly variable species, *X. compressa*, should range from Australia (including Norfolk Island) to Japan, a quite distinct one, which is also distinct from the American *X. elongata*, occurs in New Zealand.

## Family PALÆMONIDÆ.

### Genus 1. ACANTHEPHYRA, A. Milne-Edwards, 1881.

#### 1. ACANTHEPHYRA SICA, Bate.

1888. Bate, 'Challenger' Macrura, p. 739, pl. 125. fig. 1.

*Habitat.* Off Cape Turnagain, 1100 fathoms; off East Cape, 700 fathoms; and off the Kermadec Islands at 520 and 630 fathoms.

*Distribution.* This species occurs both in the Atlantic and Pacific Oceans, and from Japan in the north to New Zealand in the south, at depths varying from 200 to 2675 fathoms.

2. *ACANTHEPHYRA BRACHYTELSONIS*, Bate.

1888. Bate, 'Challenger' *Macrura*, p. 753, pl. 126. fig. 7.

*Habitat.* Off the Kermadec Islands at depths varying from 200 to 630 fathoms.

*Distribution.* Seas of Japan, Philippines, Banda, and the Falkland Islands at depths of 200-2040 fathoms.

Genus 2. *PALEMON*, Fabricius, 1798.

1. *PALEMON AFFINIS*, M.-Edwards.

1837. *Palemon affinis*, M.-Edw. *Hist. Nat. Crust.* ii. p. 391.

1852. *Palemon affinis*, Dana, U.S. Explor. Exped., *Crust.* p. 584, pl. 38. fig. 5.

1888. *Palemon affinis*, Bate, 'Challenger' *Macrura*, p. 782, pl. 128. fig. 5.

1837. *Palemon Quoianus*, M.-Edw. *Hist. Nat. Crust.* ii. p. 393.

1843. *Palemon Quoianus*, White, Dieffenb. *Voy. N. Z.* ii. p. 268.

1876. *Leander affinis*, Miers, *Cat. N.Z. Crust.* p. 85.

Bate states (*l. c.* p. 782) that this species is only distinguished from *P. squilla*, Fabr., of Europe, by having the apex of the rostrum bifid, and four teeth instead of three on the under margin. But, as Miers points out, "the number of teeth varies in a large series of specimens, while the bifid appearance is caused by the greater or less approximation of the anterior tooth of the upper series to the apex of the rostrum—also a variable character." And on this ground he unites *P. Quoianus*, M.-Edw., with *P. affinis*, an opinion I quite agree with. I have never, however, found a specimen with only six teeth on the upper margin of the rostrum, and I have examined an immense number from various parts of the Colony. The number varies from seven on the upper and three on the lower to nine and six respectively.

This is the commonest Shrimp in New Zealand, and is the only one I have seen offered for sale in the fish-shops in Dunedin, Christchurch, and Wellington.

*Habitat.* Stewart Island, dredged, 10 fathoms; east coast of Otago in rock-pools, &c., commonly between tide-marks; Akaroa, Lyttelton, Wellington, Bay of Islands, and Chatham Islands. Filhol (Miss. de l'Ile Campbell, p. 434) records it from Campbell Island.

*Distribution.* A widespread southern species, found at the Cape of Good Hope, coasts of Australia, Tasmania, and in the Falkland Islands.

2. *PALEMON NATATOR*, M.-Edwards.

1837. *Palemon natator*, M.-Edw. *Hist. Nat. Crust.* ii. p. 393.

1888. *Palemon natator*, Bate, 'Challenger' *Macrura*, p. 784, pl. 128. figs. 6 & 7.

1849. *Leander erratica*, Desmarest, *Ann. Soc. Entom. France*, ser. 2, vii. p. 87.

1860. *Leander natator*, Stimpson, *Proc. Acad. Nat. Sc. Philad.* p. 109.

1876. *Leander natator*, Miers, *Cat. N.Z. Crust.* p. 86.

This species is included by Miers among the New Zealand Crustacea on the authority

of specimens so labelled in the British Museum. I have not met with it, nor does it occur, so far as I am aware, in any of the local museums in the Colony, but, being a pelagic species of very wide distribution, it is probably quite a correct reference. At the same time, Filhol (Miss. de l'Ile Campbell, p. 434) states that Hutton has collected it in the South Island.

### Genus 3. BITHYNIS, Philippi, 1860.

#### 1. BITHYNIS ORNATUS, Olivier.

1812. *Palæmon ornatus*, Olivier, Encycl. viii. p. 660.

1837. *Palæmon ornatus*, M.-Edw. Hist. Nat. Crust. ii. p. 396.

1876. *Palæmon ornatus*, Miers, Cat. N.Z. Crust. p. 87.

This is another species of wide distribution in the seas of the southern tropical regions, and is introduced into the list of New Zealand Crustacea on the authority of Heller, who obtained it at Auckland. All Heller's identifications of New Zealand Crustacea are, however, doubtful, as the 'Novara' collections appear to have got mixed up.

I have not heard of its being found at any other part of the Colony, nor does it seem to occur in the museum collections as a local species.

### Genus 4. BRACHYCARPUS, Bate, 1888.

#### 1. BRACHYCARPUS AUDOUINI, Bate.

1888. Bate, 'Challenger' Macrura, p. 798, pl. 129. fig. 5.

This species is fully described by Bate from a single female specimen, but it is apparently common in shallow waters round the coasts. The number of teeth in the rostrum varies from eight to nine in the upper, and from four to six in the lower margin. When alive, the body of the animal is nearly transparent, the hepatic region being green. On placing the specimens in alcohol the green turns to a bright red, and numerous red star-like spots also appear on the bases of the limbs, the colours dying out after a day or two.

*Habitat.* Cook Strait, 10 fathoms ('Challenger' Exped.); Tasman and Blueskin Bays, 10 fathoms, trawled.

*Distribution.* Confined to New Zealand.

### Family NEMATOCARCINIDÆ.

#### Genus 1. NEMATOCARCINUS, A. Milne-Edwards, 1884.

##### 1. NEMATOCARCINUS UNDULATIPES, Bate.

1888. Bate, 'Challenger' Macrura, p. 801, pl. 130.

*Habitat.* North of the Kermadec Islands, 600 fathoms.

*Distribution.* Philippines and Banda Islands.

## 2. NEMATOCARCINUS GRACILIS, Bate.

1888. Bate, 'Challenger' Macrura, p. 815, pl. 132. fig. 8.

*Habitat.* North of the Kermadec Islands, 600 fathoms.

*Distribution.* Fiji Islands, 610 fathoms.

## 3. NEMATOCARCINUS SERRATUS, Bate.

1888. Bate, 'Challenger' Macrura, p. 819, pl. 132. fig. 11.

*Habitat.* Off East Cape, 700 fathoms.

This species is described from a solitary specimen. Bate says (*l.c.* p. 820), "associated with *Acantheephyra purpurea*"; but this is evidently a slip instead of *A. sica*, as the former species is found only in the Atlantic Ocean, whereas *A. sica* was trawled at the above locality.

## 4. NEMATOCARCINUS HIATUS, Bate.

1888. Bate, 'Challenger' Macrura, p. 821, pl. 132. fig. 12.

This species was constituted on a fragmentary specimen.

*Habitat.* Off East Cape, 700 fathoms.

## Family STYLODACTYLIDÆ.

## Genus 1. STYLODACTYLUS, A. Milne-Edwards, 1883.

## 1. STYLODACTYLUS DISCISSIPES, Bate.

1888. Bate, 'Challenger' Macrura, p. 851, pl. 138. fig. 1.

*Habitat.* North of the Kermadec Islands, 600 fathoms. Described from two specimens.

## 2. STYLODACTYLUS ORIENTALIS, Bate.

1888. Bate, 'Challenger' Macrura, p. 854, pl. 138. fig. 2.

*Habitat.* North of the Kermadec Islands, 600 fathoms. Described from a solitary specimen.

It is worth recording in this paper that, in 1894, the Otago Acclimatisation Society liberated specimens of *Penæus canaliculatus*, Oliv. (obtained from Sydney), in Dunedin Harbour. I made a protest at the time, using as my strongest argument to a utilitarian and unscientific body the waste of money involved in attempting to introduce a tropical species into our cold waters, for the south-east coast of the South Island of New Zealand, as far north as Banks Peninsula, is washed by a cold southerly current. But some fifty specimens were brought over and set free.

Nothing more has been seen of these Prawns, and it is very improbable that any of them have survived. But should this species hereafter be found in New Zealand waters, the fact of their having been introduced will have to be taken into account.



EXPLANATION OF THE PLATES.

PLATE 27.

Figs. 1-5. *Pontophilus australis*.

- |  |                         |
|--|-------------------------|
| Fig. 1. Front of carapace, from above. | Fig. 4. First pereopod. |
| 2. Base of first antenna.              | 5. Telson and tail-fan. |
| 3. Third maxilliped.                   |                         |

Figs. 6-12. *Alpheus socialis*.

- |   |  |
|---|--|
| Fig. 6. Part of large male specimen.                              | Fig. 9. Extremity of first pereopod of small male (from inside). |
| 7. Front of carapace of same.                                     | 10. Extremity of third pereopod.                                 |
| 8. Front of carapace of a specimen from Port Phillip (Australia). | 11. Telson and tail-fan.   |
|   | 12. Outer plate of last pleopod.                                 |

PLATE 28.

Figs. 1-2. *Betæus equimanus*.

- |                                      |                 |
|--------------------------------------|-----------------|
| Fig. 1. Carapace, viewed from above. | Fig. 2. Telson. |
|--------------------------------------|-----------------|

Figs. 3-12. *Alope palpalis*.

- |                                       |                                 |
|---------------------------------------|---------------------------------|
| Fig. 3. Portion of sternum.           | Fig. 8. Second maxilla.         |
| 4. Telson and sixth pair of pleopods. | 9. First maxilliped.            |
| 5. First antenna.                     | 10. Second maxilliped.          |
| 6. Mandible.                          | 11. Second pereopod.            |
| 7. First maxilla.                     | 12. Dactylos of third pereopod. |

Figs. 13-16. *Hippolyte bifidirostris*.

- |                        |                            |
|------------------------|----------------------------|
| Fig. 13. Ophthalmopod. | Fig. 15. Third maxilliped. |
| 14. First antenna.     | 16. First pereopod.        |

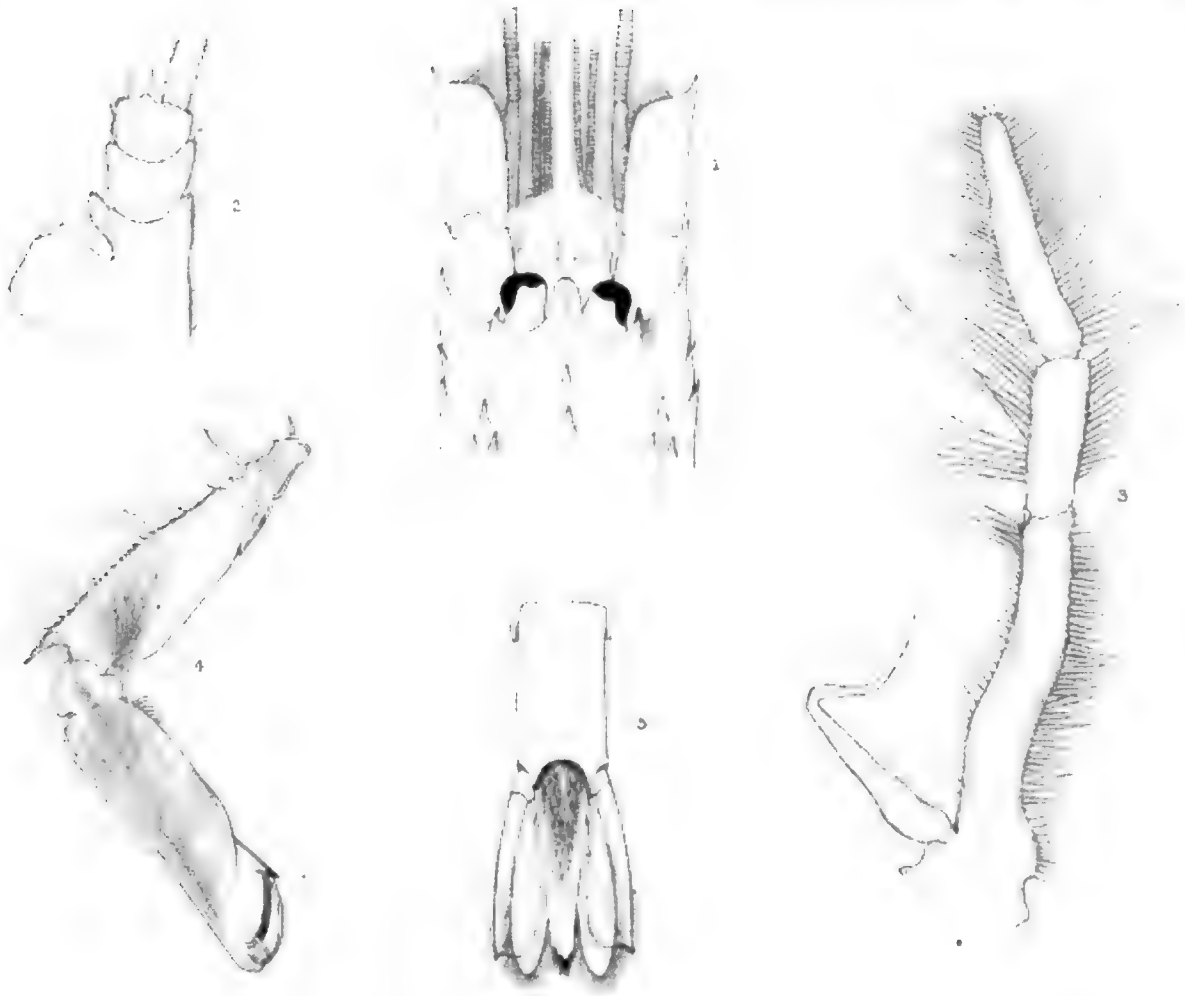
PLATE 29.

Fig. 1. *Nauticaris Stewarti*.

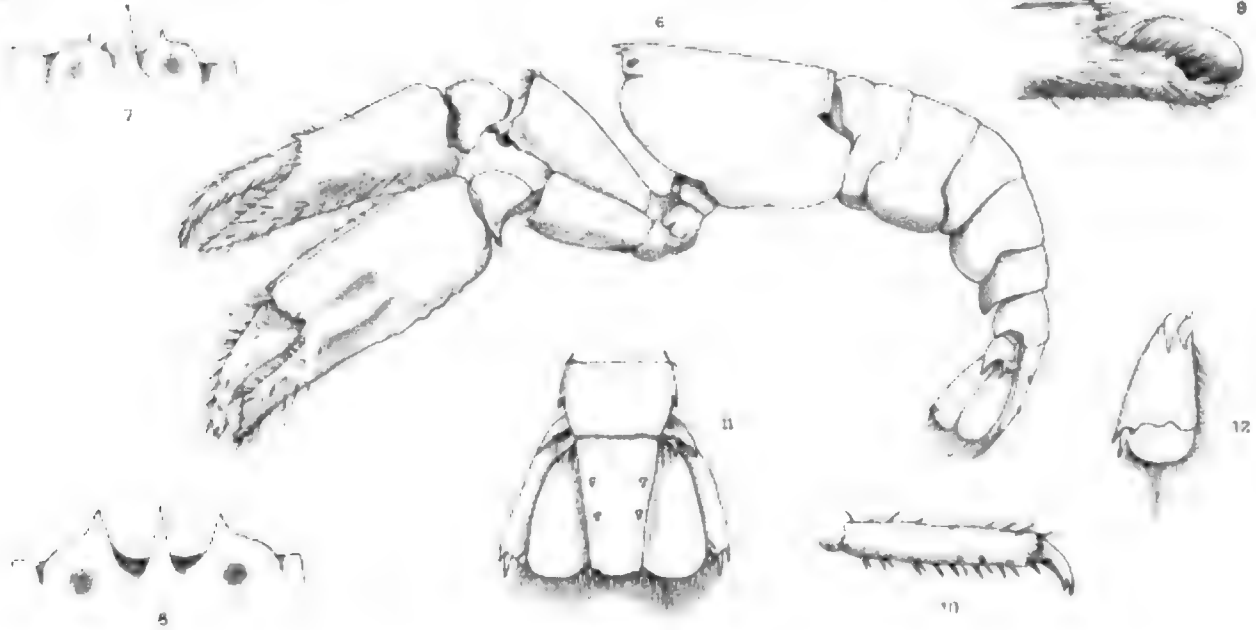
Figs. 2-13. *Xiphocaris curvirostris*.

- |                    |                         |
|--------------------|-------------------------|
| Fig. 2. Side view. | Fig. 8. Second maxilla. |
| 3. Telson.         | 9. First maxilliped.    |
| 4. First antenna.  | 10. Second maxilliped.  |
| 5. Second antenna. | 11. Third maxilliped.   |
| 6. Mandible.       | 12. First pereopod.     |
| 7. First maxilla.  | 13. Second pereopod.    |

A



B



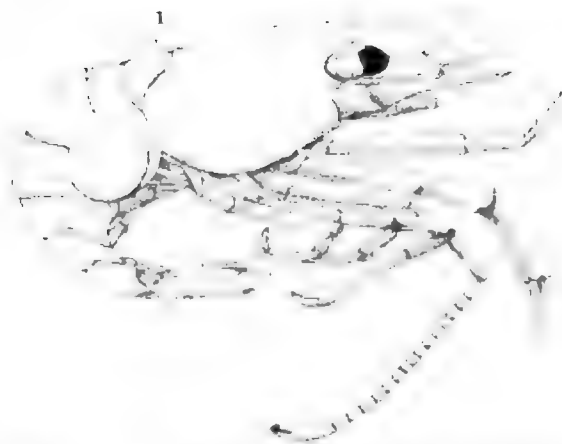
A *PONTOPHILUS AUSTRALIS* Thomson  
B *ALPHEUS SOCIALIS* Heller



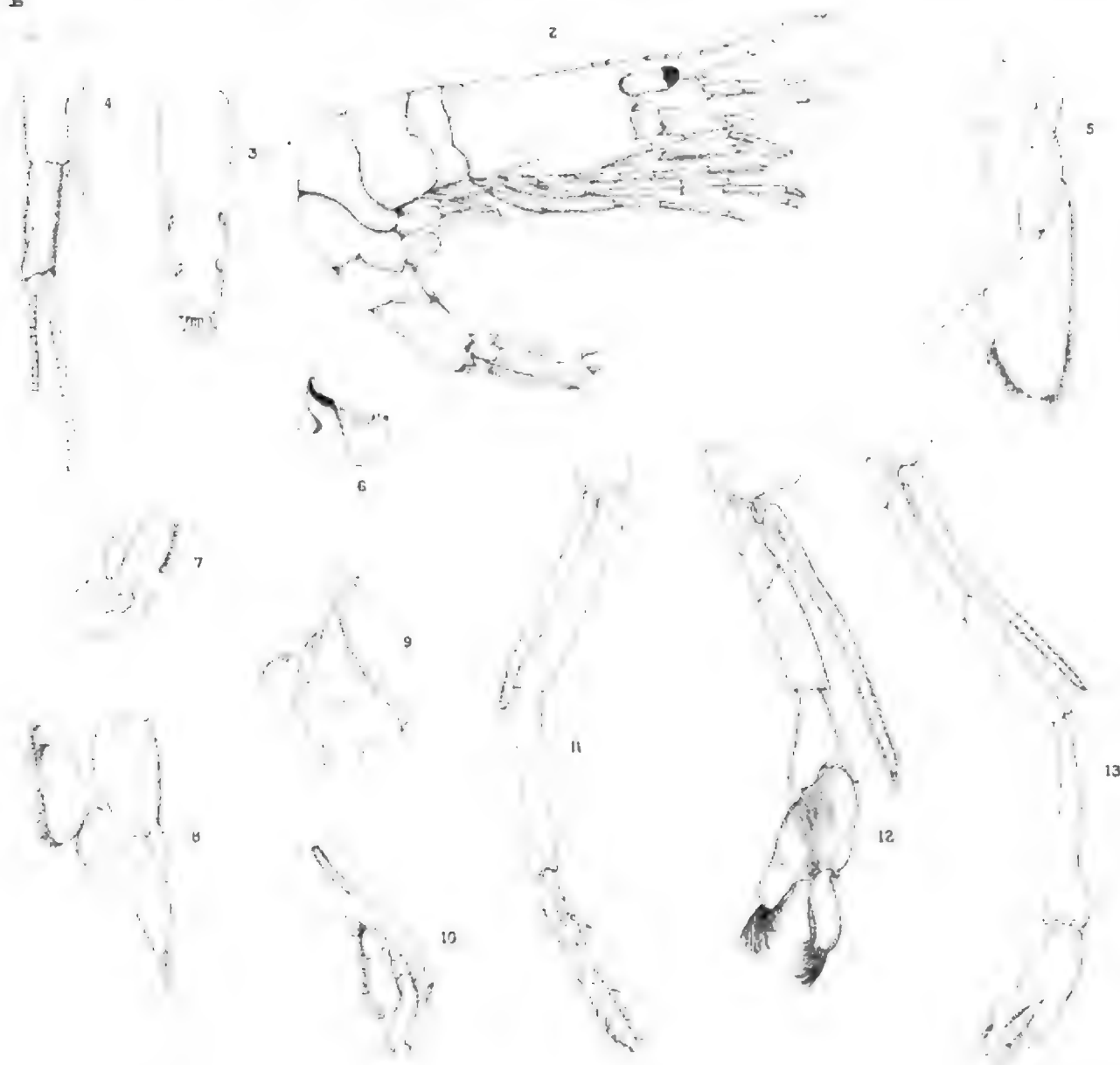
Figure 1  
A meeting with the author



A



B



A. NAUTICAPIS STEWARTI Thomson.  
B. XIPHOCARIS CINCTOSTYLA (Dana.)

J. TREMPER REID, LITH. EDIN.

XII. *On the Morphology of the Cerebral Commissures in the Vertebrata, with Special Reference to an Aberrant Commissure found in the Forebrain of certain Reptiles.*  
By G. ELLIOT SMITH, M.A., M.D., Fellow of St. John's College, Cambridge;  
Professor of Anatomy, Egyptian Government School of Medicine, Cairo. (Communicated by Prof. G. B. HOWES, D.Sc., LL.D., F.R.S., Sec. Linn. Soc.)

(With 36 Illustrations in the Text.)

Read 5th June, 1902.

IN spite of the innumerable memoirs which have been published on the homologies of the cerebral commissures in the Sauropsida and Ichthyopsida, the essential problem has practically remained untouched, and the subject still awaits a full discussion. I do not propose at this time to attempt the complete solution of this matter, but merely wish to point out the nature of the question at issue, and to bring forward some facts which seem to suggest in which direction we must seek for the full explanation.

To make clear the exact scope of this communication, I may be permitted to explain the circumstances under which it was written.

About five years ago the late Mr. Martin Woodward gave me the head of an adult *Sphenodon* (preserved in alcohol), from which I was able to obtain a brain in a sufficiently good state of preservation to be cut in a series of coronal sections. When these had been stained with lithium carmine, I was greatly surprised to find a band of commissural fibres crossing the epithelial roof of the third ventricle midway between the "dorsal" (hippocampal) and "superior" (habenular) commissures, such as I had hitherto seen only in the Lacertilia. [In the following account I shall call this commissure by the name "*aberrans*," because all the other terms in current use are highly objectionable.]

Shortly afterwards I was enabled to confirm this fact, and study the relations of the *commissura aberrans* in a series of sagittal sections, which were cut from a specimen kindly given to me by Dr. Hans Gadow of Cambridge.

Although the only contributions \* to our knowledge of the brain of *Sphenodon* which had been published at that time contained no reference to the presence of the peculiar commissure, I withheld the publication of my incomplete studies, in the hope of obtaining material which might be examined after treatment by the staining methods of Weigert and Golgi.

In 1899 Professor Arthur Dendy, for the first time, placed on record the existence of this peculiar commissural tract in *Sphenodon* †. Dendy's memoir was written in New

\* Baldwin Spencer, "On the Presence and Structure of the Pineal Eye in Lacertilia," Quart. Journ. Micr. Sci., vol. xxvii. p. 165; G. Osawa, "Beiträge zur Anatomie der *Hatteria punctata*," Archiv mikr. Anat., Bd. li. p. 587; R. Wiedersheim, Grundriss d. Vergl. Anatomie, 1893, p. 261.

† A. Dendy, "The Parietal Eye and Adjacent Organs in *Sphenodon*," Quart. Journ. Micr. Sci., vol. xlii. pp. 121 and 143.

Zealand, where it was impossible to consult all the recent literature relating to this region of the brain, and hence he used the term "commissura fornicis," which was the original name applied to this tract of fibres by Rabl-Rückhard. I might add, in passing, that this original and now discarded term is unquestionably the least objectionable of the names hitherto applied to this commissure.

In addition to devoting himself to the study of the early developmental history of the Tuatara, Professor Dendy also collected a valuable series of embryos, which were sent to Professor Howes in order that the histogenesis of the skeleton might be fully investigated. After a number of beautiful series of coronal and sagittal sections of embryos of various ages had been made by Mr. Swinnerton for this work\*, Professor Howes kindly suggested to Professor Dendy that I should study the developmental history of the nervous system in the specimens in which he was investigating the skeletal structures. Professor Dendy kindly gave his consent to this suggestion, and in addition offered to obtain specimens of properly preserved adult brains. During the year 1899 I devoted most of my vacations to the examination of this valuable material in Professor Howes's laboratory at the Royal College of Science, where these notes were written. As I left England shortly afterward, I have had no chance of seeing the material again, and as there seems little prospect of doing so in the immediate future, I am publishing in this incomplete form the most interesting observations of which I had made a record. In order to enhance the value of this, which being so imperfect is in itself slight, I have introduced into the account a series of comparative notes, which I believe will shed some light on one of the darkest and least-understood corners of the brain, and help towards systematizing our knowledge for the future.

The roof of the forebrain of *Sphenodon* presents an exceedingly irregular form (fig. 1). It consists of a thin layer of epithelium which, attached in front to the dorsal extremity of the lamina terminalis, ends posteriorly at the situation of the habenular ("superior") commissure by becoming continuous with the thicker epithelium of the parietal stalk. Its irregular course between these two points is represented on a greatly-enlarged scale in figure 2. From the upper end of the lamina terminalis ( $\alpha$ ) the epithelial layer bends downward in the third ventricle and, after being thrown into many folds, ascends again and becomes continuous with a long, narrow, irregular evagination of the roof, which is commonly known as the *paraphysis*. The irregular fold ( $\beta$ ), which is invaginated into the ventricle between the lamina terminalis and the paraphysis, is prolonged laterally on each side into a complicated fold which extends through the foramen of Monro into the lateral ventricle. As these lateral processes are known as the choroid plexuses, the fold  $\beta$  may be distinguished as the *lamina chorioidea* (generally spelt "choroidea" in English works). The paraphysis is separated from a much longer and broader outgrowth of the roof ( $\gamma$ ) by a simple transverse lamina, which is commonly called the "velum." The irregular fold  $\gamma$  is known as the "dorsal sac."

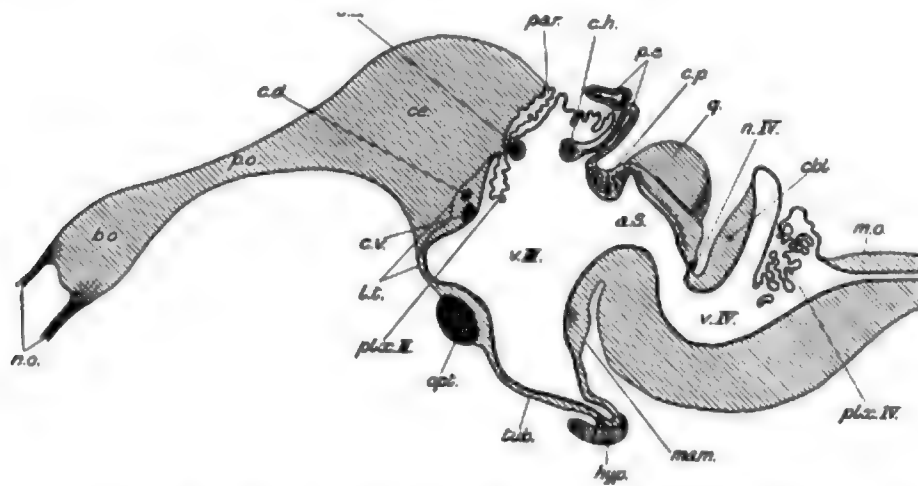
The varied nomenclature which is applied to these structures has been discussed in

\* *Vide* G. B. Howes and H. H. Swinnerton, "On the Development of the Skeleton of the Tuatara," *Trans. Zool. Soc.*, vol. xvi. (1901) part 1, for an account of the material.



Sorenson's critical review \* of the enormous mass of literature which is devoted to this region of the brain.

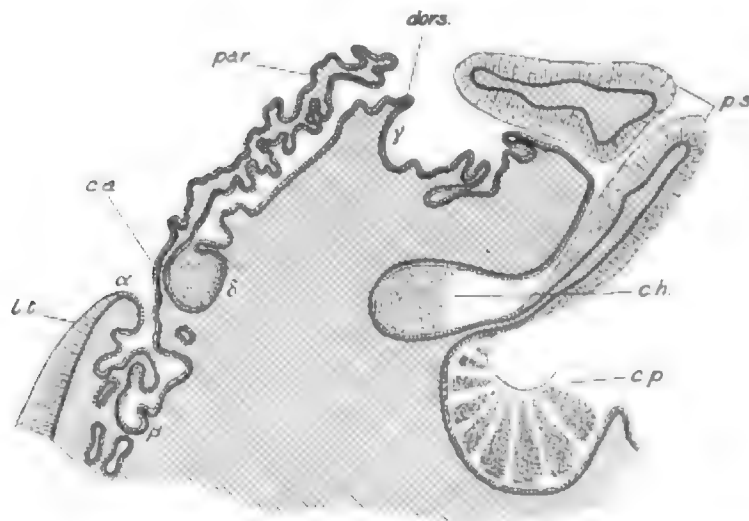
Fig. 1.



A mesial sagittal section of the brain of an embryo [Dendy's stage S] of *Sphenodon punctatum*. Magnified almost 10 diameters. Outline drawn with camera lucida.

The cerebral hemisphere and the anterior quadrigeminal body, which, of course, are not seen in a mesial section, are also represented; for explanation of abbreviations see page 500.

Fig. 2.



Semi-schematic representation of the Roof of the Forebrain in *Sphenodon*. Considerably enlarged from figure 1. Camera lucida drawing. The *commissura aberrans* is immediately in front of the letter δ.

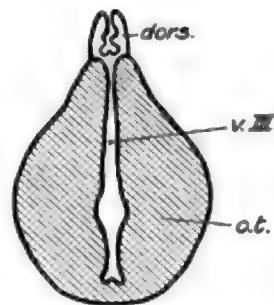
The structures just enumerated are found in almost all Vertebrates. But in the brain of *Sphenodon* there is another structure in close relationship with the roof of the third

\* A. D. Sorenson, "Comparative Study of the Epiphysis and Roof of the Diencephalon," Journ. Comp. Neurology, vol. iv. (April 1894) pp. 12-72.

ventricle. It is the rounded bundle of nerve-fibres forming the aberrant commissure lying upon the epithelium of the velum ( $\delta$ ).

If a series of coronal sections of the brain of *Sphenodon* be examined, it will be found that of the mesial structures only the lamina terminalis and that portion of the epithelial roof which lies in front of the *commissura aberrans* stand in direct connection with the cerebral hemisphere. That portion of the roof which is placed on the caudal side of the *commissura aberrans*, and which forms the dorsal sac (the so-called "Zirbelpolster" of Edinger), is connected laterally with the dorsal lips of the optic thalami. In other words, it forms the roof of the third ventricle, and is not directly connected with any part of the cerebral hemisphere. This simple relationship of the epithelial dorsal sac to the optic thalami is shown in the accompanying diagram (fig. 3).

Fig. 3.



A simple scheme to illustrate the relationships of the epithelial roof ("dorsal sac") behind the *commissura aberrans*.

But the lateral connections of the forward continuation of this epithelial roof undergo sudden and most significant changes immediately in front—i. e., on the cephalic side—of the *commissura aberrans*. This fact (which, so far as I am aware, has never hitherto been definitely formulated) might be differently stated by saying that THE COMMISSURA ABERRANS INDICATES IN THE MESIAL PLANE THE CAUDAL LIMIT OF THE ATTACHMENT OF THE CEREBRAL HEMISPHERE to the rest of the neural tube.

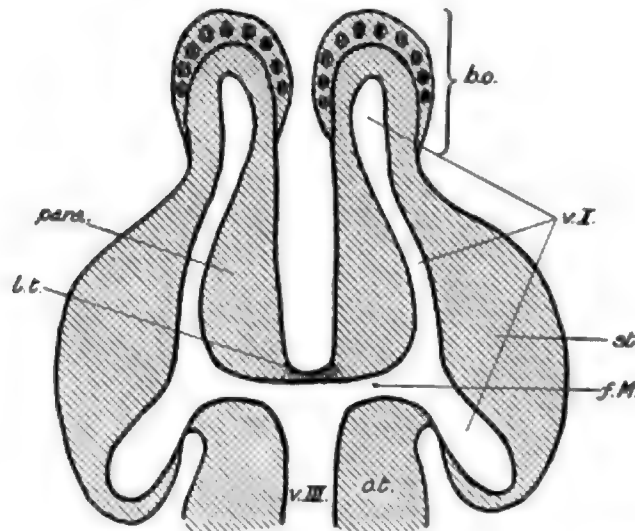
In endeavouring to arrive at some explanation of the meaning of this ambiguous commissure, as I shall attempt to do later on in this memoir, its limbic situation will be found to be perhaps its most significant feature.

Before investigating the relationships of the cephalic portion of the roof of the median ventricle, it is expedient to study the relations of the lamina terminalis and the cerebral hemisphere.

The examination of a series of horizontal sections through the brain of any Reptile or Amphibian will reveal the lamina terminalis as a narrow band connecting two large vertical masses of grey substance, which I propose to call the "*paraterminal bodies*." Each *corpus paraterminale* forms the inner wall of the anterior portion of the lateral ventricle, and extends forward from the lamina terminalis as far as the olfactory bulb or, in those cases in which the bulb is pedunculated, to the olfactory peduncle. These two large masses of neural substance are linked together by the lamina terminalis, which

extends across the mesial plane as a transverse band of an epithelial or neuroglial nature which is devoid of nerve-cells. In most cases, however, the commissures which grow across the mesial plane in contact with the lamina terminalis carry with them some grey substance (derived from the corpora paraterminalia) which forms the "commissure-bed"—a secondary thickening of the lamina terminalis.

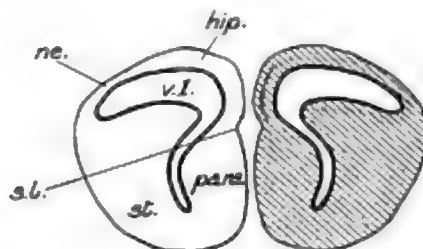
Fig. 4.



A scheme to indicate the fundamental relationships of certain portions of the cerebral hemispheres to the lamina terminalis and optic thalami: being the plan of an ideal horizontal section.

If a coronal section be made through the cerebral hemisphere of *Sphenodon*, immediately in front of the lamina terminalis, the relationship of the *corpus paraterminale* to the surrounding areas will be more readily appreciated.

Fig. 5.



A coronal section through the two cerebral hemispheres of *Sphenodon* (Dendy's foetal stage R) immediately in front of the lamina terminalis.

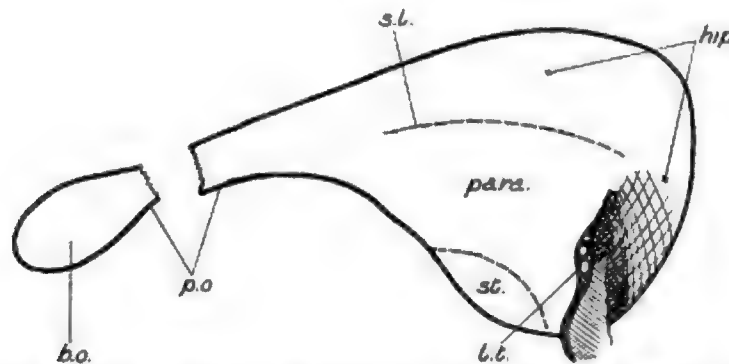
Each paraterminal body will then appear as the thick plump mesial wall of the hemisphere, which is continuous ventrally around the ventricle with the corpus striatum on the lateral aspect of the ventricle.

The upper edge of the thick paraterminal body is fused with a relatively thin portion of the wall of the ventricle, in which the nerve-cells are collected into an extremely

densely packed and regular layer, instead of being scattered irregularly in the thickness of the wall, as is the case in the paraterminal body. In the subsequent discussion it will be seen that there is little reason for hesitation in homologising the mesial portion of this thin roof the hemisphere, *i. e.* the part adjoining the paraterminal body, with the hippocampus or cornu Ammonis of the Mammalian brain. Hence I may be permitted in anticipation to call this region by the name "hippocampus." In the roof of the hemisphere the hippocampal structure passes into continuity with another cortical area which, for reasons which will appear later, I shall call "neopallium." Upon the mesial surface of the hemisphere a shallow furrow, which I shall call "*sulcus limitans*," indicates the dorsal limit of the paraterminal body and the line of junction of the latter with the hippocampus.

The mesial surface of the cerebral hemisphere in front of the lamina terminalis may now be mapped out into areas corresponding to the hippocampus, paraterminal body, and a small and ill-defined mesial portion of the corpus striatum. The accompanying sketch

Fig. 6.



The right cerebral hemisphere of *Sphenodon*.—Semi-diagrammatic representation of its mesial aspect. Enlarged.

of the mesial surface of the cerebral hemisphere in *Sphenodon* serves to indicate in a rough manner the approximate distribution of these several areas.

In the description of the mesial structures, it has already been noted that towards its upper part the lamina terminalis appears to expand into a fusiform enlargement which serves as a matrix for the dorsal and ventral commissures. If a coronal section through the brain be made in this situation, it will be seen that the two cerebral hemispheres are joined the one to the other by this matrix, or thickened lamina terminalis, which forms a bridge between the two hemispheres.

A comparison of the accompanying figure 7 (which passes transversely through the commissures and lamina terminalis) with the previous illustration, will at once reveal the identity of most of the parts of the brain exposed. Thus the relations of the "hippocampus" and "neopallium" to the paraterminal body and the corpus striatum, respectively, are unchanged. In the thickened lamina terminalis will be noted in addition the two cerebral commissures. The *commissura dorsalis* is a great U-shaped

strand, each limb of which ascends through the paraterminal body and ultimately enters the hippocampus: in the hippocampus its fibres are found scattering in the interval between the regular column of cells and the lining epithelium of the lateral ventricle.

The *commissura ventralis*, on the other hand, presents the appearance of a transverse horizontal band extending laterally into the corpora striata.

But in addition to all these structures the section passes through the *recessus opticus*, and hence opens up the third ventricle and the structures in relationship with its walls. The walls of this portion of the third ventricle consist of the most cephalic portion of the thalamic region. It may be noted here that in the region of the lamina terminalis the anterior extremity of the thalamic region fuses not only with the corpus striatum, but also with the corpus paraterminale.

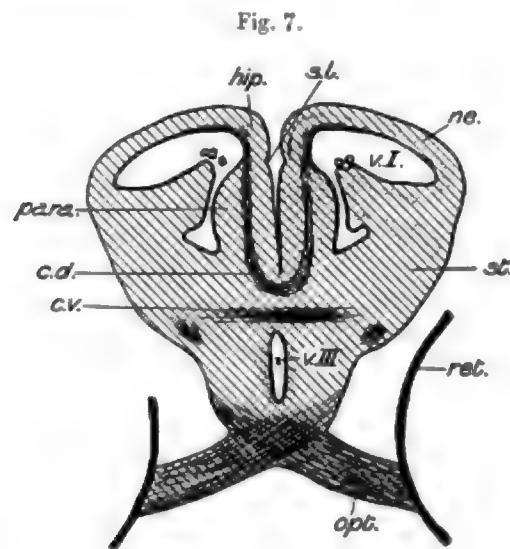


Fig. 7.  
Coronal section.—Brain of fetal *Sphenodon* (Dendy's stage R).

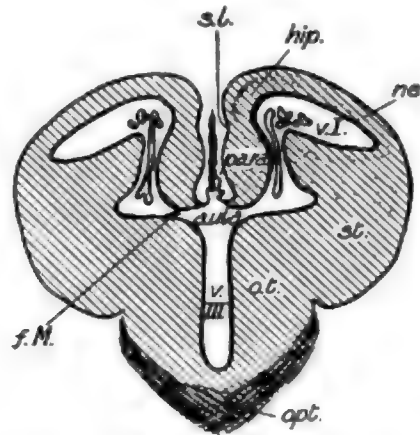
A section (fig. 8) which passes immediately behind the lamina terminalis presents many interesting points of difference when contrasted with the last figure.

As in the last figure, the relations of "hippocampus" and the "neopallium" to the corpus paraterminale and corpus striatum, respectively, are unchanged. But the ventral relationships of the paraterminal bodies have undergone a notable change. The third ventricle appears to have extended dorsally, and to have given off a lateral diverticulum on each side. This lateral diverticulum joins the lateral ventricle, and thus (in this section) completely separates the paraterminal body from the optic thalamus.

This dorsal portion of the third ventricle, or *ventriculus communis*, may be distinguished not inappropriately as the *aula*, a name introduced by Burt Wilder. The *aula* communicates on each side with the lateral ventricle by means of the foramen of *Monro*. The roof of the *aula* consists of an irregularly folded plate of cubical epithelium, and it therefore differs very much from the relatively thick neuroglial plate which forms the lamina terminalis. This roof, or *tela*, is attached on each side to the ventral lips of the

corpora paraterminalia. The typical relationship existing between the thalamus and the corpus striatum in this section calls for no description.

Fig. 8.

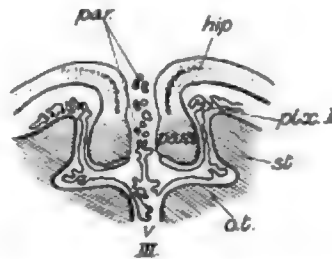


A coronal section through the brain of *Sphenodon* passing immediately behind the lamina terminalis (Dendy's foetal stage R).

If another coronal section be made midway between the upper extremity of the lamina terminalis and the *commissura aberrans*, the epithelial roof of the *aula* will be found to present a very different appearance to the simple fold which was shown in the last figure.

Upon each side an elongated and irregular fold of the epithelial roof is bulged through the foramen of Monro (or *porta*, as Wilder happily calls it) into the lateral ventricle, where it forms the lateral choroid plexus, as the accompanying figure 9 shows. A comparison of this illustration with the preceding one at once shows that this choroid

Fig. 9.



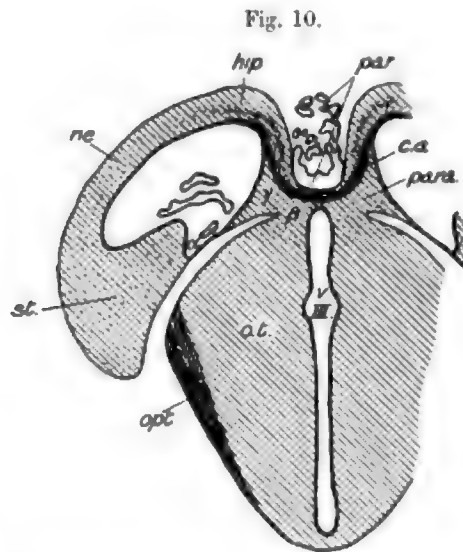
Portion of a coronal section through the brain of *Sphenodon* (Dendy's stage R), midway between the upper extremity of the lamina terminalis and the *commissura aberrans*.

plexus is not a portion of the wall of the hemisphere which has retained its embryonic character, but a part of the roof of the neural tube, which, as His has pointed out, never becomes anything else than neuroglia or simple epithelium.

The careful study of the disposition of the lateral chorioid plexus in almost any Vertebrate, or better in a series of Vertebrates, proves beyond a doubt that the choroid plexus

(at least in the region of the foramen of Monro) never forms part of the cerebral hemisphere, but is merely an appendage of the roof of the primitive forebrain. The mesial portion of the epithelial plate from which the choroid plexuses (lateral) appear to spring may be distinguished as the *lamina chorioidea*. The exact situation of this lamina is well shown in figure 2 (β). From that figure it is seen that the *lamina chorioidea* is separated from the *commissura aberrans* by the paraphysis, and this explains the presence of the paraphysis in the coronal section which has just been under consideration. It consists of a very irregular median diverticulum of the *lamina chorioidea*, which extends upwards between the two cerebral hemispheres.

A comparison of the last three figures will show that the paraterminal body diminishes in bulk as it is followed in the caudal direction. At the level of the *commissura aberrans* (fig. 10) it has assumed a triangular shape, and has established relations which are



Portion of a coronal section through the brain of *Sphecodon* (Dendy's stage R): passing through the *commissura aberrans*.

extremely peculiar and perplexing. Thus the mesial borders of the bodies in question have extended mesially, and fused the one with the other upon the roof of the third ventricle. In addition, the ventral surface of the paraterminal body is fused to the dorsal surface of the optic thalamus, producing on the whole an appearance which (especially to the student of the Mammalian brain) is in the highest degree bizarre and astonishing.

The ventrolateral angle of the paraterminal body is prolonged downward, and tapers to become continuous with a plain epithelial lamina ( $\alpha$ ), which completes the gap in the mesial wall of the hemisphere which would otherwise exist in the interval between the corpus striatum and the paraterminal body.

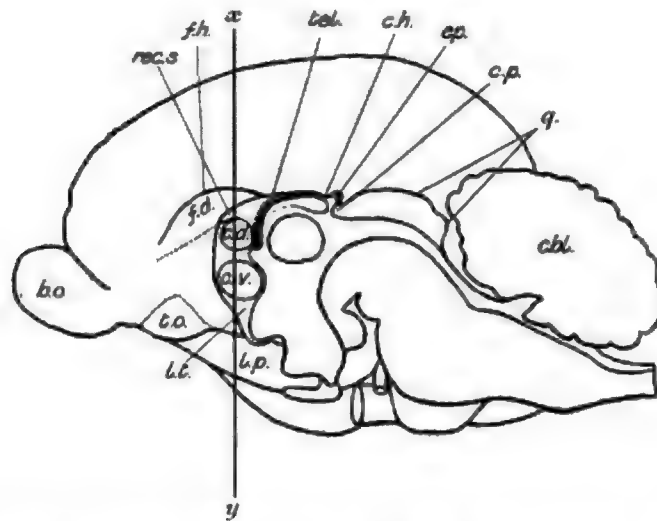
The *commissura aberrans* consists of a strand of nerve-fibres which crosses above the roof of the third ventricle in the bridge of grey matter formed by the fusion of the caudal extremities of the two corpora paraterminalia: after passing through the paraterminal



body the fibres end in the hippocampus in a manner exactly analogous to that which characterizes the *commissura dorsalis* in the most cephalic region of the hippocampus.

In 1899 I called attention \* for the first time to the fact that in the brain of *Ornithorhynchus* the roof (*tela*) of the forebrain extends forward to be attached to the upper extremity of the lamina terminalis in front of the dorsal commissure. As a result of this arrangement, a small diverticulum—*recessus superior*—of the third ventricle is formed upon the upper surface of the *commissura dorsalis*. The significance of this arrangement may possibly be not very great, but the relations of the parts which surround this little recess are most instructive when compared with those which are found in certain Reptiles, and especially the Saurians.

Fig. 11.



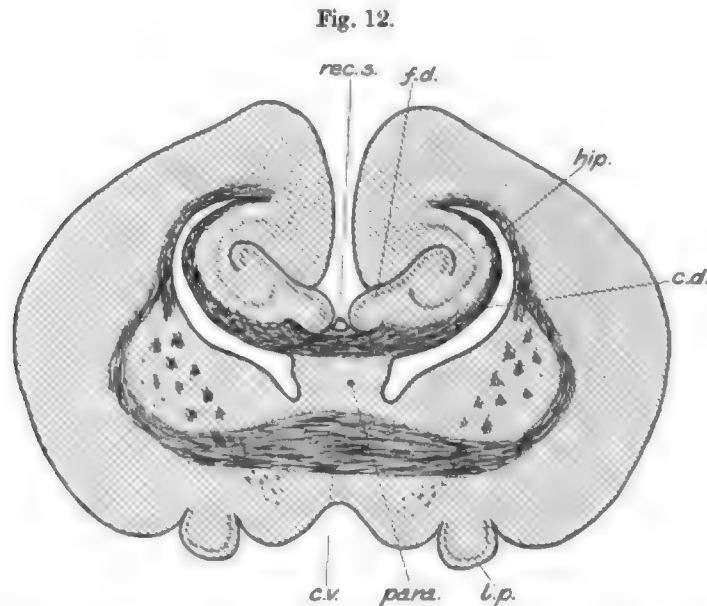
The surface of the brain of *Ornithorhynchus*, exposed by a mesial sagittal section. Magnified 2 diameters.

I have introduced here a figure from the memoir to which I have just referred, in order to make the general relations of this peculiar *recessus superior* clear, and to explain the appearances presented by sections which I intend to discuss. For a full account of the figure the reader is referred to the original description.

If a section be made through the brain of *Ornithorhynchus* (in the plane *x-y*), the cut surface will present an appearance which is reproduced upon a somewhat larger scale in the next illustration (fig. 12). The general features of this section will be familiar to those who are acquainted with the writings of Alexander Hill (*Philosophical Transactions*, 1893), Symington (*Journal of Anatomy and Physiology*, 1892), or of the present writer (*Journal of Anatomy and Physiology*, 1896). I need merely call attention to the two large commissural bands—the *commissura dorsalis*, connecting the typical hippocampal formations which are placed upon its upper surface; and the *commissura ventralis*, deriving its fibres from the whole of the other cortical areas of the brain.

\* "Further Observations on the Anatomy of the Brain in the Monotremata," *Journal of Anatomy and Physiology*, vol. xxxiii. p. 315.

In this figure, however, there are certain features which have not hitherto been represented. The most important of these is the little epithelial pocket which constitutes the *recessus superior*. It is placed upon the upper surface of the dorsal commissure between the mesial extremities of the fasciæ dentatæ. It is unnecessary for me to explain how the fascia dentata reaches this position, which to the human anatomist is so bizarre; because in several earlier communications I have explained this peculiar phenomenon (more particularly in *Journal of Anatomy and Physiology*, vol. xxxii.—especially figure 3, page 30, which represents the analogous arrangement in *Phascolarctos*).



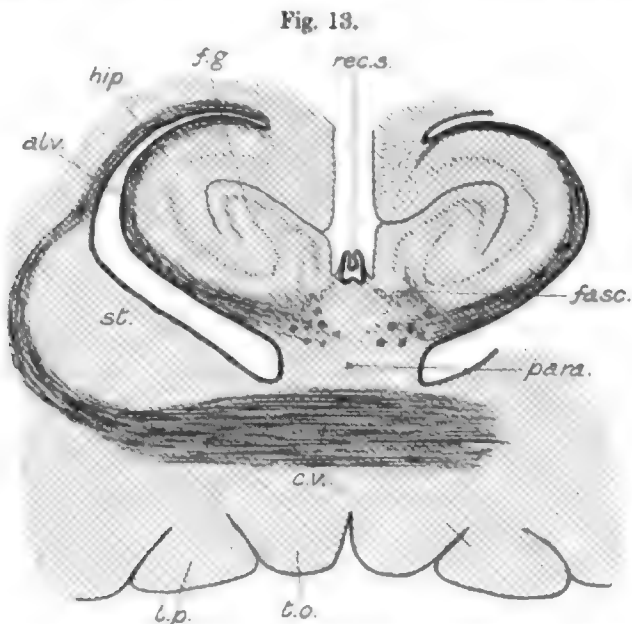
Coronal section of the cerebral hemispheres of *Ornithorhynchus*.  $\times$  about  $2\frac{1}{2}$ . The pointer from the letters *c.d.* actually ends in the *alveus hippocampi*, from which the *commissura dorsalis* is derived.

If the *recessus superior* be examined with a higher degree of magnification, its exact relations will be more readily appreciated. But certain features are more clearly demonstrated in a section which passes immediately in front of the dorsal commissure and, while missing the crossing fibres, passes through the grey matrix of this commissure. The next figure represents the superior recess from such a section (fig. 13).

In this section a solid mass of grey matter may be seen resting upon the dorsal aspect of the ventral commissure in the mesial plane, and extending upward on each side to fuse with the ventral margin of the hippocampal formation and its specialized fringe of fascia dentata. This mass of grey substance represents the posterior extremities of the corpora paraterminalia which have fused the one with the other in front of the lamina terminalis. The thickening of the lamina terminalis, which is thus produced at the expense of the paraterminal bodies, corresponds to the bridge of grey substance which forms the matrix for the two cerebral commissures.

In an earlier contribution I called this the "commissure-bed." Into this "commissure-bed" the fibres coming from the hippocampus—in other words the fornix—pass, and

many of them assume a longitudinal direction and associate themselves either with the post-commissural group (which forms the *columnar fornix*) or the precommissural group of fibres [*vide* Journal of Anatomy and Physiology, vol. xxxii. pp. 36 *et seq.*].



Part of a coronal section through the cerebral hemispheres of *Ornithorhynchus*, to show the relation of the paracommissural body to the hippocampus.

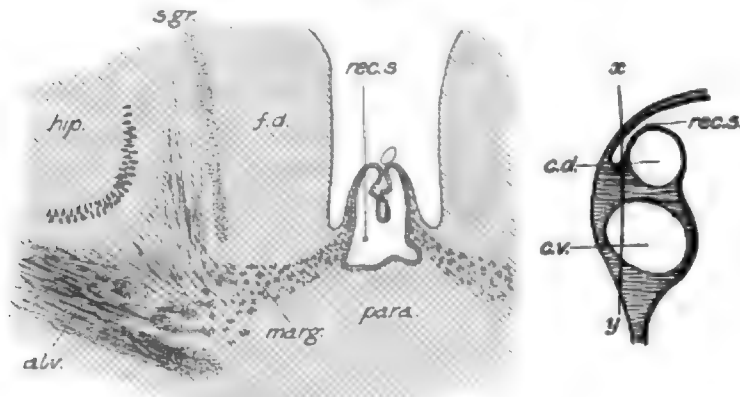
The *recessus superior* in this section rests upon the upper surface of the "commissure-bed," and presents an oblong shape. It is lined with simple cubical epithelium: its roof consists of a simple epithelial layer, and its characters resemble those of the rest of the roof (*tela*) of the third ventricle of which it forms the cephalic extremity; it is invaginated into the cavity of the superior recess to form the anterior extremity of the mesial choroid plexus—the "*diaplexus*" of Burt Wilder: the lateral walls of the recess are thickened by a small quantity of grey substance derived from the paraterminal bodies, and in this grey substance longitudinal fibres belonging to a peculiar set of fornix-fibres which are found at the ventral margin of the fascia dentata are found. These fibres belong, in all probability exclusively, to the group which I have called "*fasciculus marginalis*" (Journ. of Anat. and Phys., vol. xxxii. p. 38). In the next figure these features are shown upon a much larger scale (fig. 14).

The *recessus superior* exists and presents similar features in the brain of *Echidna*, and therefore it will be legitimate to institute comparisons between the adult *Ornithorhynchus* and certain fœtal stages of *Echidna*, with a view to the explanation of certain earlier fœtal stages of *Ornithorhynchus*. Such comparative studies are necessary, because it has been impossible to obtain a complete series of fœtal stages of *Platypus*.

If sections be made through the brain of a fœtal *Echidna* (at the age when the spines are just making their appearance in the skin), it will be found that a section passing through the two cerebral commissures will present features (fig. 15) which, on the whole, so closely resemble those of the adult *Ornithorhynchus* just considered, that it is

unnecessary to describe them in detail. But there are certain features in the region of the *recessus superior* which reproduce the condition found in the Sauropsida more nearly than does that of the adult Monotreme: in addition, the hippocampal formation is very

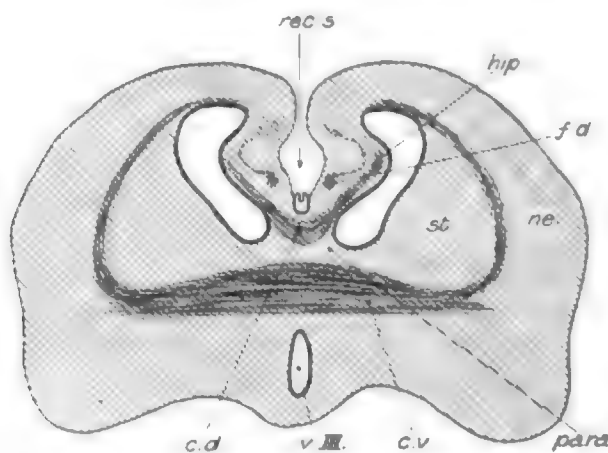
Fig. 14.



Greatly enlarged representation of part of a coronal section of the brain of *Ornithorhynchus*, to show the recessus superior and the adjoining structures. The letters *marg.* refer to the fasciculus marginalis, labelled *fasc.* in the other figures. The adjoining diagram is an enlarged part of fig. 11, to explain the plane (*x-y*) in which the section was cut.

much simpler than it is in the adult, and its exact relations to the paraterminal body less ambiguous. Such a section is roughly represented in figure 15, and the regions

Fig. 15.



A scheme of a coronal section of the brain of a very young *Echidna*, greatly enlarged.

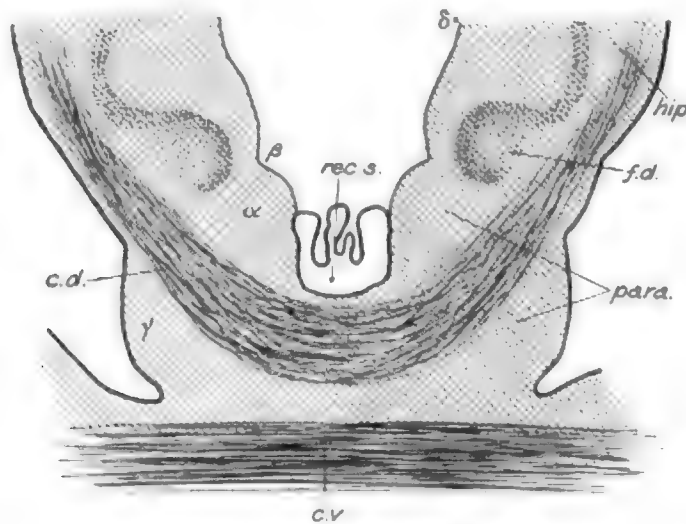
surrounding the *recessus superior* have been reproduced again upon a larger scale in another figure (16). The former illustration needs no further description, and I may turn at once to the consideration of figure 16.

In many minor points the condition in the foetal *Echidna* differs from that found in the adult *Ornithorhynchus* (and *Echidna*). Instead of the lateral walls of the superior recess being slightly thickened with grey matter derived from the paraterminal body,

the little recess will be found to be walled on each side by the whole mass of the paraterminal body, a large part of which ( $\alpha$ ) intervenes between the *recessus superior* and the ventral margin of the hippocampal formation. [I use the term "hippocampal formation" here in preference to "fascia dentata," because the latter body is obviously in the process of formation as a specialization of the lower extremity of the hippocampus.]

At the dorso-mesial angle of the hemisphere the neopallium will be found in a state of transition. The scattered nerve-cells are becoming collected into a compact column, which is readily recognized upon the mesial wall (after comparison with the adult brain) as the layer of pyramidal cells of the hippocampus. This layer of cells is already undergoing a lateral bending, but it is a significant fact that only the very slightest furrow

Fig. 16.



Scheme drawn from a coronal section through the brain of a young *Echidna*, which had been stained with lithium carmine.

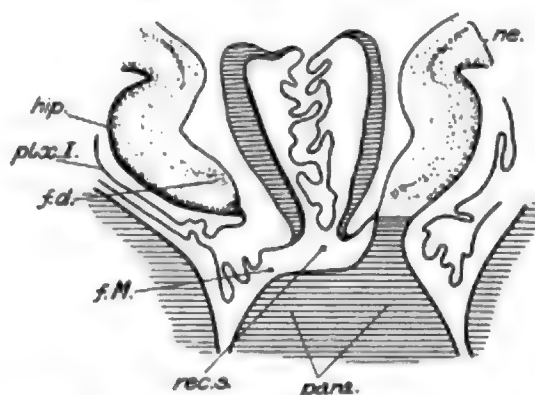
has yet made its appearance upon the mesial wall ( $\delta$ ). It is hence clear (as Hochstetter has shown) that the supposed furrow called "*Bogenfurche*" by Schmidt and "*Ammons-furche*" by Mihalkovics, which makes its appearance at a much earlier stage of development, cannot have anything to do with the true hippocampal fissure, which at this late stage is only just beginning to appear. In fact the slight furrow  $\delta$ , which is the first representative of the hippocampal fissure, is really due to the peculiar inrolling of the hippocampal formation which takes place *pari passu* with the development of the fascia dentata. The latter arises (see fig. 16) as a rapid proliferation of the ventral extremity of the column of cells which elsewhere develops into the layer of pyramidal cells. As these cells increase in number at a rapid rate, the surface area corresponding to them grows much more rapidly than the deeper regions, and becomes bent up into the peculiar pouch-like shape which the fully developed fascia dentata always presents in transverse section in the adult brain. This rapid growth in superficial extent seems

to determine to a large extent the peculiar shape of the hippocampal formation and the presence of the hippocampal fissure.

If it were pertinent to the subject of this communication, I might introduce here a large mass of data in support of these statements regarding the morphogenesis of the hippocampal formation [*vide* "The Fascia dentata," Anatomischer Anzeiger, 1896], and in support of Hochstetter's contention that the hippocampal fissure is a much later feature to make its appearance than the supposed "Bogenfurche," and that the latter has a purely post-mortem existence. I have, however, referred to this question only to point out that the fascia dentata makes its appearance comparatively late in the development of the brain\*, and is derived from the hippocampal formation by a specialization of its ventral edge.

Before leaving this section I wish to call attention to a furrow ( $\beta$ ) which separates the paraterminal body ( $\alpha$ ) from the hippocampal formation, and which I may call "*sulcus limitans [hippocampi]*." Most writers on the Reptilian brain regard the sulcus  $\beta$  as the homologue of the *Bogenfurche* ( $\delta$ ): this drawing (fig. 16) shows how erroneous such a contention is.

Fig. 17.



Scheme of a section through the *recessus superior* of a foetal *Ornithorhynchus*.

A section through the *recessus superior* of a foetal *Ornithorhynchus* (fig. 17), at a much earlier stage than the *Echidna* just considered, shows the "neopallium" (*ne.*) joining the hippocampus (*hip.*) at the dorso-mesial angle of the hemisphere just as it does in *Echidna*; but there is no definite fascia dentata, although a slightly exuberant mass of cells (*f.d.*) represents the earliest phase of its development. [The other features of this section do not concern us here and have been described elsewhere. "The Brain of a Foetal *Ornithorhynchus*," Quart. Journ. Micr. Sci. vol. xxxix. p. 181.]

In the light of the facts which this brief examination of the relations of the paraterminal body and hippocampus has revealed, it is interesting to examine the condition of the analogous parts of the brain in Reptiles. For this purpose I have deliberately chosen the brain of a Saurian, not because I suspect any close phyletic relationship between the Saurians and the Monotremata, but because the arrangement of the homologous regions in the two types of the brain is so clearly identical, that the comparison between the two becomes an extremely simple matter. The question whether this

\* The foetus under consideration had in other respects attained to almost the adult type, and yet the fascia dentata is in the primitive condition shown in the figure.

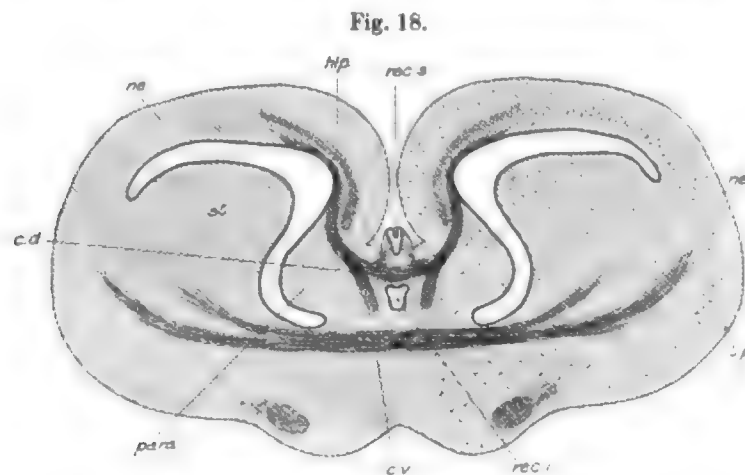


undoubted identity of arrangement is to be attributed to a close genetic relationship, or to an evolutionary convergence, does not come within the scope of this enquiry: it is sufficient that the homology is so clear as to be indisputable.

Of a large number of Sauropsidan brains which I have examined, I have chosen that of a common Australian *Hydrosaurus*, because it lends itself so admirably to exact comparison with the Monotreme brain.

If a section be made through the brain of this Monitor in a plane corresponding to that which was made through the Prototherian brains which have just been considered, a state of affairs will be found which it is easy to interpret after comparison with the foetal and adult Monotreme arrangement.

In this section (fig. 18) two commissural bands are found disposed according to a plan



Coronal section of cerebral hemispheres of *Hydrosaurus*.

which is analogous to that of the Monotreme. The question whether these dorsal and ventral commissures are not merely analogous but also homologous to the corresponding commissures in the Monotreme will be discussed subsequently, but I may for the present call attention to the similarity of their disposition.

I may remark, in passing, that no writer who has treated of this question, even though the conclusions at which he arrives are diametrically opposed to my own, has refused to admit the fact of the correspondence in position of these commissural bands in the Reptile and Monotreme. [As an example, I might refer to the writings of Osborn, 'Morphologisches Jahrbuch,' Bd. xii. p. 223, and numerous other instances might be quoted.]

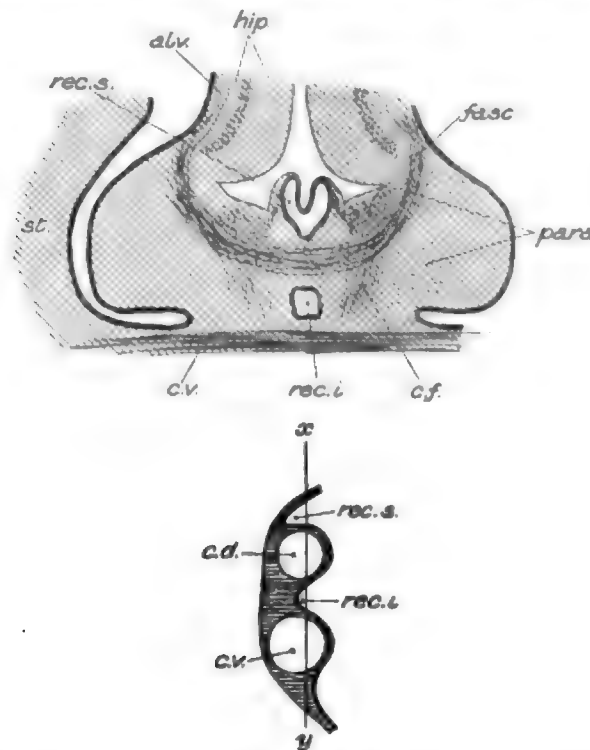
Upon the upper surface of the ventral commissure, in the section under consideration, two bulky masses of grey substance are found joined across the middle line by bridges of grey substance. These grey masses are the posterior extremities of the paraterminal bodies, which are relatively much larger than the corresponding bodies in the Monotremata. In the next figure they are represented upon a larger scale. Upon the upper surface of the paraterminal body a *recessus superior* is found resembling in all its features that of the adult *Ornithorhynchus*. Thus it presents an epithelial roof, invaginated to form a mesial choroid plexus—"diaplexus" of Wilder. Its lateral walls are thickened



with grey substance derived from the paraterminal body, as in the Monotreme; and in this grey mass a number of longitudinal nerve-fibres are found which constitute the mesial elements of a larger series of fibres which are found in that part of the paraterminal body which clearly corresponds to the region distinguished as  $\alpha$  in the foetal *Echidna*. There can be no valid reason for refusing to regard these fibres as the homologues of the "*fasciculus marginalis*" of the Monotreme. The fact that a foramen or "intercommissural recess" is found in the "commissure-bed" in the Reptile and not in the Monotreme, need cause no difficulty, because a sagittal section of the lamina terminalis at once shows the unimportant nature of this feature: on the other hand, the

Fig. 19.

Portion of a coronal section through the brain of a Monitor (*Hydrosaurus*).



Scheme of lamina terminalis to show the plane of the section  $x-y$  above.

presence of such a recess between the columns of the fornix—the *recessus triangularis* of Schwalbe—is a well-known fact in the case of the brains of the Meta- and Eutheria.

The dorsal edge of the paraterminal body is fused with the lower extremity of a thin portion of the wall of the hemisphere, which presents a peculiarly distinctive histological structure. It is characterized by the presence of a very regular closely-packed column of cells, which is placed somewhat nearer the ventricle than the surface of the hemisphere. The component cells of this column are moderately large pyramids, the apices of which are directed toward the surface; from the basal aspect of each cell an axis-cylinder process passes off and contributes to the formation of a layer of nerve-fibres

between the cellular column and the ventricular epithelium. From this layer of nerve-fibres the *commissura dorsalis* is derived. In the brain of *Hydrosaurus* the limits of this peculiarly distinctive histological formation are so sharply defined, and its features, in spite of slight variations in different parts of the column, are so distinctly differentiated from the rest of the hemisphere, that there can be no reasonable ground for hesitation in regarding the column as one indivisible organ or natural cortical formation. By this statement I mean that whatever conclusion concerning the homologies of the ventral (or any other) portion of the column the subsequent discussion may yield, will apply of necessity to the whole of this peculiar cortical formation. In *Hydrosaurus* the area in question begins at the upper border of the paraterminal body, forms the whole of the mesial wall of the hemisphere above this body, and extends on to the dorsal aspect of the hemisphere and forms almost half of the roof of the lateral ventricle. It then terminates almost as suddenly as it began, and gives place to a more scattered pallial formation which forms the lateral portion of the roof.

If the general relations of this medio-dorsal cortical area in the Reptile to the paraterminal body, to the *recessus superior*, to the *commissura dorsalis*, and to the longitudinal fibres in its neighbourhood be compared with those which a study of the embryonic and adult Monotreme brain has revealed, the agreement in the arrangement of all these several parts in the two types is too close and too obviously identical to be a mere coincidence or chance resemblance. There can be no reason to doubt that the *commissura dorsalis* in the Reptile is *mainly*, if not wholly, the homologue of the corresponding commissural band in the Monotreme, and that the medio-dorsal cortical formation in the Saurian is the homologue of the hippocampal formation of the Mammal.

The study of the behaviour of this supposed hippocampus, with which the subsequent parts of this memoir are largely concerned, affords an indisputable argument in favour of the hypothesis that this medio-dorsal cortex cannot be anything else than the strict homologue of the hippocampus of the Mammalian brain. This view is by no means new, for, since Spitzka made this suggestion concerning the homology of the mesial wall of the hemisphere in 1880\*, a similar interpretation has been from time to time maintained by other writers, many of whom have independently arrived at the same conclusion. I shall attempt to prove, however, that these views have never yet passed beyond the stage of mere suggestions, because they have not been founded upon any reliable evidence, and it may be remarked that in several cases they have been rejected by their authors in favour of others on very slight provocation. Indeed, none of the writers to whom I allude have had sufficient confidence in the truth of their suggested homology to draw the logical conclusions which the adoption of such a view must entail. Thus none dare to speak of all the fibres coming from their "hippocampus" as fornix.

The reasons which led Spitzka to regard the mesial cortex as hippocampus I cannot, in the absence of a first-hand knowledge of his memoir, definitely formulate; but the conflicting statements of his views by Brill and Strasser (*vide infra*) are sufficient to show that his argument could not have been very conclusive or well-founded. According to Strasser (Merkel and Bonnet's 'Ergebnisse,' Bd. ii. 1892, p. 579), Spitzka placed the fascia dentata upon the LATERAL aspect of the hippocampus (*sensu stricto*). If this be so, the committal of such a fundamental error is of itself sufficient to render the author's

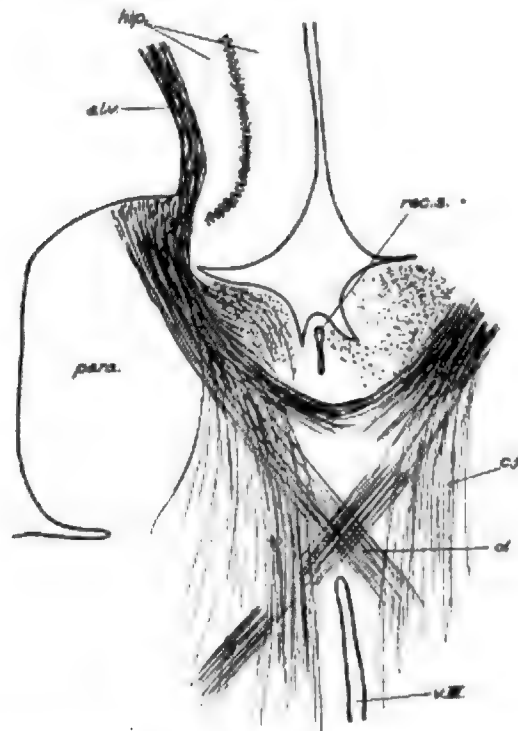
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\* Spitzka, "The Brain of Iguana," Journal of Nervous and Mental Disease, 1880. I know this work only from the writings of Brill, Edinger, Herrick, Meyer, and others.

suggestions utterly nugatory. In addition, the fact that Spitzka called the commissure of his "hippocampi" "*corpus callosum*" \* seems to indicate a distrust of his own suggestions.

In 1888 Edinger definitely homologized the medio-dorsal cortical formation in a number of Reptiles as the "*Ammonsrinde*," or "*Ammonsformation*," and in a series of excellent figures of coronal sections of the brain of a Saurian he leaves no doubt as to the meaning of his written statements; for he labels the medio-dorsal cortex in these illustrations "*Cortex Ammonis*" †. It is instructive to quote his reasons for this conclusion, because they are logical and well-founded, and have a considerable interest in view of the fact that their author was led into a singular error five years later and gave up his earlier and correct belief for another view. In 1888 he wrote (*op. cit.* p. 116):—"Das betreffende Rindenstück [medio-dorsal cortex] muss man als erstes Auftreten der Ammonsrinde [hippocampus] in der Tierreihe ansehen. Die Ammonsformation wird charakterisirt durch ihre Lage über dem Hemisphärenrand, durch den ihr anlagernden Fornix und durch den auf ihn folgenden Plexus choroides. Sie enthält also bei ihrem ersten auftreten alle die Elemente welche später, wenn auch durch Windungen und dergleichen verwischt, das charakterische Ammonshorn bilden."

Fig. 20.



Part of a transverse section through the cerebrum of *Hydrosaurus* (immediately in front of the commissures), showing the decussating fornix-fibres (a).

This is not the first representative of the cornu Ammonis in the animal series, for it can be distinctly recognized in a large number of the Ichthyopsida; nor is it accurate to speak of part of the paraterminal body as the "fornix." But in spite of these inaccuracies, Edinger's argument is perfectly legitimate; for the position [at least of the caudal part] of the medio-dorsal cortex in the mesial wall of the

\* According to Edinger, *Abhandl. d. Senckenberg. Gesellschaft*, 1896, p. 314.

† L. Edinger, "*Untersuchungen über die vergleichende Anatomie des Gehirns—I. Das Vorderhirn*," *Abhandlungen der Senckenbergischen naturforschenden Gesellschaft*, 1888, Taf. iii. figs. 21, 22, 23, and 24.

hemisphere and its relation to the choroid plexus are valid reasons for regarding the cortex in question as the representative of the cornu Ammonis, or hippocampus, of the Mammalian brain.

Having homologized this caudal portion of the medio-dorsal cortex with the hippocampus, Edinger, with good reason, did not hesitate to regard the cephalic extension of the same histological formation as also part of the hippocampus. But the amazing feature of Edinger's memoir is that, after having recognized this medio-dorsal cortex as the hippocampus, the author does not hesitate to call the commissure which is derived from it by the name "*corpus callosum*." And this name has clearly not been employed in the wider sense as including the hippocampal fibres, because upon page 117 this statement is found:—"Ueber der Commissura anterior liegt (fig. 22) die grosse von Osborn mit Recht als Balken bezeichnete Mantel-Commissur. Ihre Fasern stammen aus dem Gebiet der grossen Zellen in den dorsalen Wand nach aussen der Ammonsrinde."

The figure 22, to which Edinger refers, represents *all* these commissural fibres springing not "*aus dem Gebiet nach aussen der Ammonsrinde*," but from the hippocampus itself, and, so far as my own observations go, this figure is perfectly accurate. In other words, the great majority, if not all, of the fibres of the dorsal commissure in the Reptile spring from the hippocampus, and therefore cannot be called "*corpus callosum*."

It is perfectly incomprehensible why Edinger, who definitely recognized the hippocampus and the fibres of the dorsal commissure springing from it (as his figures clearly show), should have called the commissure "*corpus callosum*." He seems to have deliberately gone beyond his facts in order to make a spurious pretence of agreement with Osborn. Now Osborn (*Morphologisches Jahrbuch*, 1887, Bd. xii. *cit.*) did not for a moment deny the origin of the fibres of his so-called "*corpus callosum*" from the mesial cortex in the Reptile. The fallacy of his argument was his failure to recognize this mesial cortex as hippocampus. Edinger clearly recognized the latter fact, but failed to see the logical outcome of his suggestion. He seems to have utterly ignored the facts which he had himself clearly demonstrated, for the sake of a pretended confirmation of the conclusions of Osborn.

Two years after the publication of this memoir of Edinger's, Brill published a brief communication\*, with a view to make known the work of Spitzka, and to record a series of original observations upon the brain in the Lacertilia, Ophidia, Crocodilia, and Chelonina. He argued that the position of the medio-dorsal cortex in the hemisphere and its histological structure showed its homology to the fascia dentata. He regarded the rest of the dorsal cortex as the hippocampus and subiculum cornu Ammonis. And in support of this hypothesis he propounded (upon wholly inadequate grounds) the statement that "*the fascia dentata is more primitive than the hippocampus*," and therefore not unnaturally "*forms the greater part of the Reptilian hemisphere*." In the introduction to this discussion I pointed out that the fascia dentata is a specialization of the ventral edge of the pre-existing hippocampus, which makes its appearance relatively late in the ontogenetic history of the Mammalian brain. Moreover, it consists of a peculiar modification of the surface (only) of the hippocampus, as I have shown elsewhere ("*The Fascia dentata*," *Anatomischer Anzeiger*, Bd. xii. 1896, p. 124). So that it cannot exist apart from the hippocampus.

In its typical form the fascia dentata is found only in the Mammalia, whereas the hippocampus can be certainly recognized in all the Sauropsida, Amphibia, and Dipnoi, and even in some still lowlier vertebrates. It is therefore preposterous to argue that "*the fascia dentata is more primitive than the hippocampus*," as Brill does.

In 1890 C. L. Herrick began the publication of a series of contributions to the morphology of the brain. The first of these memoirs which deals with the question at issue appeared in the first number of '*The Journal of Comparative Neurology*,' which this prolific writer founded in 1891. It deals

\* N. E. Brill, "The True Homology of the Mesal Portion of the Hemispheric Vesicle in the Psauropsida [*sic*]," *Medical Record*, March 29, 1890, pp. 343-345.

mainly with the brain of a Lizard (*Sceloporus*), a Snake which he does not name, and a Turtle (*Aspido-nectes*). In the Lizard, he says (p. 15), there is in the occipital lobe "an undoubted homologue of the hippocampus." In the Snake he says that "the portion homologous to the hippocampus is relatively highly differentiated"; and that even "the portions corresponding in cellular structure to the fornicate and uncinate gyri may be distinguished"! By these statements, which are nonsense as they stand, the author really means to record a would-be important fact. In a later communication upon the brain of *Didelphys* ("The Cerebrum and Olfactories of the Opossum," Journ. of Comp. Neurology, vol. ii. 1892) the author calls the fascia dentata the "gyrus uncinatus," the hippocampus the "gyrus fornicatus," and the hippocampal fissure the "splenialis fissure." The monstrous nature of such use of well-known terminology does not seem to have been appreciated by their author, for when Dr. Hill called his attention to the unusual application of these terms he naively remarked that "obscurity was needlessly introduced . . . by using the terms *gyrus fornicatus* and *uncinatus* for parts which are more often named *cornu Ammonis* and *gyrus dentatus* respectively, without discussion of homologies concerned" (Journal of Comp. Neurology, vol. iii. (1893)! In the light of these remarks it is possible to understand his statement of 1891, which I have already quoted above. According to this interpretation, it is possible to distinguish in the hippocampus of the Black Snake a marginal region corresponding to the fascia dentata and another region corresponding to the hippocampus (*sensu stricto*).

In this (1891) memoir, Herrick gives a good description of the cephalic portion of the real hippocampus, which he calls "fronto-median lobe" (p. 18), since he does not recognize its hippocampal nature. This is very surprising, because he records the fact that the so-called "occipital cortex" (which he regards as the whole of the hippocampus) and his "fronto-median lobe" are not only continuous, but present similar histological features. He does not hint at the fact that the "fronto-median lobe" may also be hippocampus; and his apparent ignorance of the earlier memoirs of Spitzka, Edinger, and Brill explains the lack of the suggestion from outside sources, which his own histological studies should have supplied.

The reasons which dictate this distinction between the caudal and the cephalic regions of one uniform and indivisible histological formation are probably to be found in the fact that the caudal portion corresponds in its topographical position to the hippocampus in most Mammals. Yet, strange to relate, neither the study of *Didelphys* nor the knowledge of the work of Edinger and others appear to have had any influence upon Herrick's interpretation; for, in spite of the fact that the hippocampus extends forward in the Marsupial, and in spite of the suggestions of Edinger regarding the hippocampus in Reptiles, he, in his later works, still clings to his original view that it is confined to the caudal part of the hemisphere. And for this reason it is not surprising to find that, after denying in a positive and formal manner the hippocampal nature of his "fronto-median lobe," he regards its commissure as the true corpus callosum—for this is the natural and logical inference to be drawn from his erroneous interpretation.

In 1893 Edinger returned to the discussion of the problem of the hippocampus in the Reptilia\*, and practically renounced the view (undoubtedly correct) which he had published in 1888. In the later work he attempted to extend the region of the hippocampus to the *lateral* aspect of the hemisphere in the Chelonia, being apparently deceived by the spurious resemblance of an inverted cortical area in this situation to the Mammalian hippocampus. Not only did he commit this extraordinary error, but also the less excusable one of locating the fascia dentata upon the lateral aspect of the hemisphere *external to the hippocampus* (*cornu Ammonis*). It is only just to add that he subsequently appreciated the groundlessness of these suggestions, and amply acknowledged his error (Abhandl. d. Senckenberg. Gesell. 1896, p. 326).

\* L. Edinger, "Reichapparat und Ammonshorn," Anat. Anzeiger, Bd. viii.

I may pass over the consideration of the works of the brothers Ramon y Cajal, of Köppen, Schulgin, Botazzi, Maracino, and Milia, because they contribute nothing fresh to the morphological problem under discussion, and as they have been reviewed by Edinger (Abhandl. d. Senckenberg. Gesell. 1896, pp. 318-319).

In 1892 a most important contribution to the discussion of the problem made its appearance, its author being Adolf Meyer ("Ueber das Vorderhirn einiger Reptilien," Zeitsch. f. wiss. Zoologie, Bd. lv. p. 63).

Meyer attempted to institute comparisons between the Reptile and the foetal, rather than the adult, Mammal. • He called the paraterminal body the "septum lucidum," but this loose application of a term, which is strictly associated with a special modification of the dorso-caudal extremity of the paraterminal body, and which is found only in the more highly organized Mammalia, can hardly be regarded as happy, and at the outset prejudices the chance of an exact comparison. He described a furrow in certain Reptiles, which marks the line of demarcation between the paraterminal body and the cortical area, which I have referred to as hippocampus. This furrow is the *fissura limitans hippocampi*, and Meyer homologized it with the furrow which separates the so-called "Randbogen" into outer and inner arcs. While this comparison with the somewhat problematical "Randbogen" of the Mammalian foetus is unfortunate, he further compared the cortical portion of the mesial wall of the Reptilian brain with the "outer Randbogen" of the mammal, but he did not commit himself to any more precise homology than this.

He declined to call the dorsal commissure "corpus callosum," as Osborn, Edinger, and most writers before him had done. The reason for this is not that the fibres arise from the region which he compared with the "outer Randbogen," but because the commissure in question is situated in the lamina terminalis, and not in a secondary fusion of the mesial walls of the hemisphere. This argument is fallacious, as it is based upon a misconception as to the real position of the primordial corpus callosum.

In 1896 Edinger once more reconsidered the whole question of the morphology of the mesial wall of the hemisphere in Reptiles; and, as I have already mentioned, he then corrected the errors which he committed in 1893. He approached the study of this subject again, not only with the much wider knowledge which his own researches has yielded, but with the benefit of the results of the work of Spitzka, Brill, Herrick, and especially Meyer, on the Reptilian brain; and of Symington, Hill, and myself, upon the brain of the Proto- and Metatheria. Von Kölliker also, in the same year, added the weight of his authority to the controversy, but apparently merely as the interpreter of the data collected by the writers quoted above. Indeed, the view with which the names of Edinger and Kölliker became associated in 1896 is so plausible and so insidiously deceptive that it is necessary to state it at some length, with the objections to it. In 1894 Kölliker stated that some of the uncrossed fibres of the fornix in the Mammalian brain are derived from the gyrus fornicatus—that is, from a part of the neopallium beyond the limits of the hippocampus\*. In reviewing this work shortly afterwards, Edinger† used the term *Randwindung* as a synonym for "gyrus fornicatus"; and elsewhere he subsequently used the term "*gyrus limbicus*" in the same sense. I mention this specifically, because both of these terms had been previously used as synonyms for the *indusium griseum*, which is not a part of the gyrus fornicatus, but is composed mainly of the vestigial supracallosal portions of the hippocampus (vide Schäfer, 'Quain's Anatomy,' ed. x. vol. iii. pt. 1, 1893, p. 159). In 1896 Edinger spoke of the *gyrus limbicus* in mammals as the frontal continuation of the "*Ammonsrinde*," "*welche nicht mehr eingerollt ist und über dem Ventrikel liegt*." From the reference to the inrolling, it is clear that the author cannot be using the term "*Ammonsrinde*" in the literal sense of "*gyrus hippocampi*" (which is

\* "Ueber den Fornix longus von Forel," Verhandl. d. anatom. Gesellschaft in Strassburg (Anat. Anz. Bd. ix. p. 45, Ergänzung).

† "Leistungen auf dem Gebiete der Anatomie des Centralnervensystems," Schmidt's Jahrbücher, Bd. cxxvi.



really in continuity with the gyrus fornicatus \*), but as a synonym for the more usual name "*Ammonshorn*," i. e. cornu Ammonis or hippocampus. He further added: "Ich halte es für wahrscheinlich, dass in dem Rindengebiete, welches bei den Reptilien als Ammonsrinde bezeichnete wurde, die Elemente des Gyrus limbicus und der Ammonsrinde gegeben sind" ("Untersuchungen über d. vergl. Anatomie d. Gehirns. 3. Neue Studien über das Vorderhirn der Reptilien," in Abhandl. d. Senckenberg. Gesellsch., 1896). Thus, while he was clearly using the term "gyrus limbicus" in the sense of the "gyrus fornicatus" he spoke of this structure as the forward continuation of the hippocampus, as if the latter were identical with the pallial area confusedly known as the "hippocampal gyrus." The first quotation is so vaguely expressed that one might readily imagine the author to be using the term "gyrus limbicus" (or "Randwindung") in the sense of the *inlusium* or vestigial hippocampus, as Schäfer does in 'Quain's Anatomy.' In this case the statement would be quite intelligible; but this interpretation the author never intended, for while in the second quotation (*supra*) he referred to the "Gyrus limbicus und der Ammonsrinde," in his 'Vorlesungen,' which were published contemporaneously, he called the *inlusium* (*striae longitudinales Lancisii*) the forward continuation of what he somewhat rashly terms the "schon im Ammonshorn atrophischen Windung, des Gyrus dentatus." (L. Edinger, 'Vorlesungen über den Bau der Nervösen Centralorgane des Menschen und der Thiere,' 5th ed., Leipzig, 1896.)

It is clear from the foregoing quotations that Edinger, in renouncing his erroneous views of 1893, did not revert to his original belief of 1888. On the contrary, he stated distinctly that the region which he had previously called cornu Ammonis, and of which he now speaks as the "Ammonsrinde," contains the elements not only of the "Ammonsrinde" or hippocampus, but also of the gyrus limbicus (or gyrus fornicatus). Some inkling of the meaning of these extraordinary views is obtained from Edinger's definition of the *fornix longus* as that "welcher aus demjenigen Theile der Randwindung, welcher nicht zum Ammonshorn sich einrollte, aus dem Gyrus limbicus" (Vorlesungen, p. 210). In this statement he was evidently attempting to harmonize the morphology of the cerebral cortex with the supposed grouping of the fibres springing from it. In other words, he argued that the gyrus fornicatus is the anterior continuation of the hippocampus, because the fornix is derived posteriorly from the latter and anteriorly from the gyrus (according to the belief of Kölliker [*vide supra*] and Edinger). Again, he stated (*op. cit.* p. 168) that in the higher Mammals, as a consequence of the development of the corpus callosum, the fibres of the fornix coming from the hippocampus become separated from those which come from the more anteriorly placed part of the "Randwindung" (meaning the gyrus fornicatus).

By thus introducing the idea of a "Randwindung" or gyrus marginalis, which includes both gyrus fornicatus and hippocampus, Edinger obviously intends to establish a morphological justification for Kölliker's belief in the origin of the fornix in part from the gyrus fornicatus. Whether any fibres of the fornix ever have any such origin is extremely doubtful (*vide* "The Fornix Superior," Journal of Anatomy and Physiology, vol. xxxi. p. 90).

Kölliker in his 'Gewebelehre' (*op. cit.* 1896) approved of Edinger's interpretation, and translated the vague and somewhat cryptic language of the latter into a clear statement, free from all ambiguity. He thus distinctly, though unintentionally, reduced the argument to a *reductio ad absurdum*!

Thus Kölliker, whilst speaking of the Reptilian brain ('Gewebelehre des Menschen,' Bd. ii., zweiter Hälfte, 1896, p. 825), writes:—"Edinger hat schon eine Andeutung, ob dieser Fornix der Reptilien nicht dem *Fornix longus* der Säuger entspreche, die ich voll unterstützen möchte. Die mediale Wand des Vorderhirnes der Reptilien entspricht ja nicht nur Ammonsfalte, sondern auch dem *Gyrus fornicatus* der Säuger, aus welchem der *Fornix longus* entspringt. Ein *Fornix inferior* kann bei den Reptilien kaum vorhanden sein, da auch das Ammonshorn, in welchem derselbe entspringt, nicht gebildet ist."

This means that Edinger and Kölliker regarded the cortex of the mesial wall of the Reptilian

\* I mention this point specifically because elsewhere Edinger has on several occasions confused the hippocampus and gyrus hippocampi.



hemisphere as partly homologous with the gyrus fornicatus, *i.e.* with a cortical area of the mammalian brain which is *not* hippocampal. And yet both of these writers spoke with complete approval of the view that the dorsal commissure, which springs from this mesial wall, is the *psalterium* or hippocampal commissure. But if the mesial wall be partly gyrus fornicatus, its commissure cannot be the *psalterium*, but must be the corpus callosum. There can be no doubt that the homology of the mesial wall of the Reptilian hemisphere with the hippocampus is correct; and the comparison with the Monotreme brain, which I instituted in an earlier part of this memoir, shows conclusively that *no part of the mesial wall of the Reptilian hemisphere can be regarded as the homologue of the gyrus fornicatus.*

It is strange that when Edinger held the mesial cortex of the Reptilian hemisphere to be hippocampus, he called its commissure not "*psalterium*" but "*corpus callosum*" (*op. cit.* 1888); and that when, eight years later, he changed his view and regarded it as including not only the hippocampus but a non-hippocampal pallial area, he called it not "*corpus callosum*" but "*psalterium*," with a singular disregard for consistency.

A comparison of the Reptilian cerebral hemisphere with that of the fœtal and adult Monotreme conclusively demonstrates that the whole of the mesial wall of the former which is placed above the paraterminal body, together with a considerable part of the roof of the hemisphere, represents unquestionably the mammalian hippocampus, *and nothing else.*

Although the Reptilian hippocampus is not so highly differentiated as its Mammalian homologue, in that its margin is not yet definitely specialized to form a *fascia dentata*, I utterly disagree with Kölliker in the statement that in the Reptilia "*das Ammonshorn nicht gebildet ist.*"\*

The arguments for the recognition of the medio-dorsal cortex in the Sauropsida as the hippocampus may be concisely summed up in the following manner. A comparison of the brain of the Eutheria with the Meta- and Prototheria shows that in both of the latter lowly orders of Mammals—widely as they are undoubtedly separated the one from the other—the hippocampus has a much more extensive distribution than in the former. Instead of being confined to the caudal portion of the hemisphere, it extends forward as far as its morphologically anterior pole; and as a search in the analogous region of the Eutherian hemisphere has revealed vestiges of this cephalic extension of the hippocampus, it is natural to conclude that THE ANCESTORS OF THE MAMMALIA POSSESSED A HIPPOCAMPUS EXTENDING FORWARD UPON THE MESIAL WALL OF THE HEMISPHERE TO ITS CEPHALIC POLE, *i.e.* TO THE NEIGHBOURHOOD OF THE OLFATORY PEDUNCLE. The presence of a peculiarly distinctive histological formation in the brain of the Reptile exhibiting not only the identical relations of the Prototherian cornu Ammonis, but also possessing a structure which corresponds to one phase through which the Mammalian hippocampus passes in its ontogenetic development, can be rightly interpreted in only one way. These reasons for thus homologizing the mesial cortex in the Reptile have hitherto never been categorically formulated, and they constitute the only legitimate ground upon which such an interpretation can be based. The early suggestions of Spitzka and Brill, and Edinger's extraordinary memoir of 1893, are little more than guesswork. The value of the legitimate argument of Edinger in 1888 was utterly destroyed by his later contributions in 1893 and 1896. And the sound work of Adolf Meyer left the question in too undecided a state to be regarded as in any way settling the question.

A hippocampus presenting the general features already briefly indicated exists in all classes of Reptilia, but the details of its structure vary somewhat in the different families. In all Reptiles the hippocampus forms not only the whole of the mesial wall of the hemisphere above the paraterminal body, but also part of the dorsal surface of the hemisphere. In many of the Chelonians, such, for example, as *Emys*

\* Much of the foregoing discussion has already been published in a short memoir entitled "*Further Observations upon the Fornix, with Special Reference to the Brain of *Nyctophilus*,*" *Journal of Anatomy and Physiology*, vol. xxxii. 1898. It is repeated here in order to make the argument complete and intelligible.

*europæa*, the cells of the hippocampus are much more diffusely scattered than in *Hydrosaurus* and, to a lesser degree, in *Sphenodon* also. This more diffuse scattering of cells points to the more primitive condition of the hippocampus exhibited in the Amphibian brain. Osborn has given such an excellent representation of it in *Emys*, that it is quite unnecessary for me to do this here (Osborn, *Morph. Jahrb.*, Bd. xii. Taf. xiii. fig. 16). In *Chelone*, however, the cells are much more compactly arranged, so as to form a regular column which presents a close resemblance to that found in *Sphenodon*, which I have already represented\*.

In the Chelonia, Crocodilia, and Rhynchocephalia the characters of the distinctive column of cells of the hippocampus are practically uniform throughout the whole length of the column; whereas in the Lacertilia, and especially in the Ophidia, the cells become much more numerous and considerably smaller in size in the neighbourhood of the paraterminal body. This fact is now well-recognized, and has been successively noted by Herrick, Edinger, Meyer, and myself among many others; and the condition has been admirably represented in the excellent figures which accompany Edinger's memoir of 1888 (*loc. cit.*) and Meyer's of 1893 (*loc. cit.*).

In the Chelonia, no such alteration in the characters of the ventral extremity of the hippocampal column of cells can be detected, nor am I able to detect any trace of such a change in the brain of *Sphenodon*.

This peculiar feature of the hippocampus in the Saurians is significant. For it points to a more rapid proliferation, resulting in the production of a large mass of cells of small size, in a position analogous to that in which the fascia dentata has been found to develop, by a similar process of rapid proliferation and small-cell formation, in the Mammal. But it may be argued that the fascia dentata in the Mammal is a group of cells set quite apart from the hippocampal column of pyramidal cells. The developmental history of the fascia dentata, at which I have briefly hinted in the Monotreme, and which follows a similar course in the placental Mammal, shows that the fascia dentata, or rather its "stratum granulosum," is originally the ventral (or inner) extremity of the column of pyramids which becomes separate at a later period of development. This process of separation can be actually seen in the adult brain of any Monotreme or Marsupial—for in these Orders the fascia dentata becomes reduced to very insignificant proportions at the cephalic extremity of the hippocampus; and as its cells are thus brought into line with the stratum of pyramidal cells of the hippocampus proper, the picture of the Saurian condition is complete (*vide* "The Fascia dentata," *Anat. Anzeiger*, 1896). It is not surprising to find that this differentiation of the hippocampal column of cells is not found in all Reptiles, when we recall the fact that in the Mammal the fascia dentata is late in making its appearance. And it is of interest to note (although it is not quite pertinent to this discussion), that, just as the fascia dentata is the last part of the hippocampal formation to make its appearance, so it is the first part to dwindle and disappear in the retrogressive changes which involve the anterior portions (supra- and precommissural) of the great hippocampal arc in the Eutheria, leaving a hippocampal vestige devoid of fascia dentata (*vide supra*; also *Trans. Linn. Soc. ser. 2, Zool.*, vol. iii. 1897, pp. 47-69; also *Journal of Anatomy and Physiology*, vol. xxxii. 1897).

The problem of the meaning of this peculiar change resulting in the development of the fascia dentata presents itself for solution. It is an extremely difficult question, which does not permit of being definitely settled in the present state of our knowledge. But the following suggestions may form a tentative hypothesis until such a fuller knowledge is forthcoming.

In the Reptile large numbers of nerve-fibres stream from the bulbus olfactorius into the neighbouring area of hippocampus. In the Monotreme and Marsupial the corresponding fibres become collected mainly at the ventral margin of the hippocampal formation (see *Journal of Anatomy and Physiology*,

\* Good figures of the brain of *Chelone mydas* will be found in Edinger's memoir in the *Abhandl. d. Senckenberg. naturf. Gesellsch.*, 1896, Taf. 2, figs. 5 & 6.

vol. xxxii.), and form the *fasciculus marginalis*. Olfactory impulses coming from the olfactory bulb are thus poured into the ventral fringe of the hippocampus, and this fringe becomes specially modified to form a large mass of "receptive cells"—the fascia dentata. In other regions of the brain modifications of superficial cells are found in regions in which sensory paths impinge upon the cerebral cortex. This is very slightly shown in the general cortex of higher Mammals because the sensory fibres are widely scattered; but it is most pronounced upon the surface of the *lobus pyriformis* (*vide supra*): here a very rich supply of incoming olfactory fibres covers the surface of the lobe, and the superficial cells become specially modified to form the layer of "double pyramids," which is such a characteristic feature of this region. In a similar manner a peculiar cortex is developed in the *tuberculum olfactorium* (*vide supra*).

It would seem, therefore, not unreasonable to suppose that as the fibres coming from the olfactory bulb began to collect at the ventral margin of the hippocampus, the latter region became specially modified to form as the fascia dentata a receptive organ for olfactory impulses.

In the Saurian brain a similar tendency is shown, and hence it follows that the small-celled ventral portion of the Saurian hippocampus should be regarded at least as the physiological, if not the strict, homologue of the Mammalian fascia dentata. In all the Saurians studied, the hippocampal formation comes to an abrupt termination upon the dorsal surface of the hemisphere; and the characteristic column of cells ceases, and its lateral extremity is separated from the rest of the cortical region of the brain by a pronounced hiatus. There is no reason for regarding the regions which are placed beyond this hiatus as constituting part of the hippocampus. The mesial half of the roof of the hemisphere is considered to be hippocampus because it is part of the one circumscribed histological formation, concerning the homology of the mesial part of which there can be no question; and there is no valid reason for not extending this interpretation to the whole formation. But when this typical structure comes to an end, it is only logical to infer that a region beyond the hippocampus has been attained. Now, by comparison with the Mammalian condition, it is clear that this cortical area beyond the hiatus must represent the neopallium, to which I have already referred in the Mammalian brain.

In the Mammal, however, the transition from hippocampus to neopallium is usually a more gradual process than this abrupt method which characterizes the Saurian; and if an analogy for this be desired, it will be found in the Chelonia and Rhynchocephalia, where the regular hippocampal column *gradually* gives place in the roof of the hemisphere to the scattered arrangement which is characteristic of the neopallium. In the earlier figures illustrating coronal sections through the hemispheres of *Sphenodon*, this gradual transition from hippocampus to neopallium has been shown.

The fibres which arise from or terminate in this hippocampus must be regarded as the fornix (in the sense in which I defined this term: "The Relation of the Fornix to the Margin of the Cerebral Cortex," *Journal of Anatomy and Physiology*, vol. xxxii. 1897): the Reptilian fornix, like its Mammalian representative, consists of a *fornix transversus* (Forel) or hippocampal commissure (*psalterium*, *lyra*, *fornix-commissure*), and a *fornix longus* (Forel) composed of descending post-commissural fibres (*columna fornicis*) and "pre-commissural fibres" of Huxley.

The uncrossed fibres (or *fornix longus*) need not be further considered at present, but the crossing fibres (*fornix transversus*) are of such great morphological importance in the discussion of the arrangement of the cortex, that they cannot be dismissed in this summary fashion.

The fibres which spring from the hippocampus and proceed across the mesial plane to enter the hippocampus of the other hemisphere cannot be regarded otherwise than as the homologues of the commissure variously known in mammals as *psalterium*, *lyra*, *commissura fornicis*, *commissura hippocampi*, *commissura cornu Ammonis*, *fornix transversus*, as well as by other names. This commissure is regarded as "hippocampal," not by reason of any particular relation it may present to the lamina terminalis [compare Meyer's reasoning], to the recessus superior [compare the writings of Osborn, Herrick, and many American and German writers], to the roof of the forebrain or to the foramen of Monro, but because its fibres are derived from the hippocampus. Stated thus directly, this truism may seem too

obvious to need formal presentation; but a glance at the past history of this discussion would appear to show that the inference does not naturally suggest itself to most writers; and that in deciding the question of homology, the great majority of investigators have made use of criteria which may readily be shown to be either utterly false or of limited applicability.

In the foregoing descriptions it has been demonstrated that a large strand of fibres coming from the hippocampus crosses to the corresponding region of the other hemisphere in the lamina terminalis and forms the dorsal commissure. The fact that the morphological relations of this commissure are identical with those of the dorsal commissure in the Monotreme, which is known to be of purely hippocampal origin, undoubtedly lends support to the contention that the dorsal commissure in the Reptilian brain is also a commissure of the hippocampi, *i. e.* the *psalterium*. But such an argument can only be of subsidiary value. The only essential reason for regarding the dorsal commissure as being hippocampal, and not a true "corpus callosum," must be the demonstration of its origin from the hippocampus. So far as I am aware, no investigator, with the solitary exception of Ramon y Cajal, has ever seriously attempted to claim an origin of any fibres of the dorsal commissure from the pallial area beyond the hippocampus. Edinger, it is true, appeared to do so in his first contribution to this discussion (*op. cit.* 1888), but, as I have already pointed out, his statements are not supported by his figures. And the internal evidence of his memoir seems to point to the statement merely as an attempt to harmonize his conclusions with the plausible and sweeping generalization of Osborn.

When Osborn himself argued in favour of the existence of a "corpus callosum" in the Reptilia, he did not trace any fibres of the dorsal commissure beyond the medio-dorsal cortical plate. He was led to the erroneous belief in the presence of the corpus callosum, because he did not recognize in the medio-dorsal plate the true hippocampus (H. F. Osborn, "The Origin of the Corpus Callosum," *Morpholog. Jahrbuch*, Bd. xii.). The same remarks apply to the earlier observations of Stieda ("Studien über das Centralnervensystem der Reptilien," *Zeitschr. f. wiss. Zoologie*, Bd. xxv. 1875).

Rabl-Rückhard, however, would not homologize the dorsal commissure in the Alligator with the corpus callosum, and gave it the neutral name "*commissura pallii anterior*"\*. His reason for this hesitancy was that he regarded it as corresponding neither in position with the corpus callosum, nor with what one should regard as the primitive stage of the great Mammalian commissure. He somewhat doubtfully suggested its homology with the commissure of the fornix, but gave no valid reasons for his belief.

In his numerous contributions, to which reference has already been made, Herrick regarded the dorsal commissure as a true "corpus callosum," for the reason that he refused to admit the homology of the medio-dorsal plate of cortex with the hippocampus.

Then, again, it was the relation of the dorsal commissure to the lamina terminalis, rather than its origin from the region which he compared to the "outer Randbogen," which led Adolf Meyer to refuse the title "corpus callosum" to the dorsal commissure in 1893 (*op. cit.*). In order to justify his position Meyer, in 1895, brought forward some rather arbitrary criteria of a "corpus callosum" (which I shall discuss later), but they added little to the force of his original argument.

It is somewhat surprising to find that in 1896 Edinger (*loc. cit.*) regarded the dorsal commissure (which he now calls the "*commissura pallii anterior*" after Rabl-Rückhard) as a *psalterium*, although he regarded the origin of this commissure as being homologous not only with the hippocampus but also with the gyrus fornicatus of Mammals. He attributed his change of belief to the work of Adolf Meyer (*op. cit.*) and the writer ("The Cerebral Commissures in the Mammalia," *Proceedings of the Linnean Soc. of N.S.W.* 2nd series, vol. ix.), and very properly argued that, as the commissural link between the hippocampi, it must represent the *psalterium* (Edinger, *op. cit.* 1896, p. 371). But in this passage he seemed to forget that elsewhere in the same memoir (p. 384 *inter alia*) he refused to admit that the

\* "Ueber das Centralnervensystem der Alligators," *Zeitschrift für wiss. Zoologie*, Bd. xxx. 1878.

cortical area in question was hippocampus only, and concluded by regarding it as also representing the gyrus fornicatus.

His lack of consistency is almost as pronounced as it was eight years earlier, when he called the medio-dorsal cortex "hippocampus" and its commissure "corpus callosum." In 1896 he almost reversed the process by calling the commissure "psalterium," but declining to admit that its area of origin is simply "hippocampus."

I have dwelt at great length and with, I fear, much repetition upon the views of Edinger, because his opinion has been widely accepted from time to time by writers of all nationalities as authoritative, and hence, in all recent memoirs and text-books which treat of the comparative anatomy of the brain, the dorsal commissure in Reptiles and Amphibians is called "psalterium." It only needs a writer to come forward (as Flower did in 1865, in the controversy regarding the commissures in the Monotremes and Marsupials) and indicate the weakness of the basis for the general belief, to cause a general revulsion to the conviction of the presence of a corpus callosum in all Vertebrates. For so history might repeat itself. But although Edinger's argument lacks cogency and consistency, the conclusion at which he arrived regarding the dorsal commissure is undoubtedly correct. For the fibres of the dorsal commissure must be hippocampal, i. e. *psalterium*, because they spring from the hippocampus.

In this discussion I have not yet referred to the possibility of the fibres of the dorsal commissure arising from a wider cortical area than the hippocampus. The only author who, so far as I am aware, directly admitted this possibility is Pedro Ramon y Cajal ('Investigaciones micrograficas en el Encephalo de los Batraceos y Reptiles,' Zaragoza, 1894). I am only acquainted with this work at second hand from the excellent figure which Edinger reproduces (*op. cit.* 1896, p. 319). In this figure a group of fibres is represented passing upward from the dorsal commissure (which he calls "corpus callosum") through the paraterminal body and hippocampus to end in the pallial area beyond the latter. These fibres are labelled "Mehr lateral aufgezweigte Balkenfasern für die laterale Rindenplatte." In no specimens which I have examined have I been able to satisfy myself that any such fibres came from the dorsal commissure and extend beyond the hippocampus. It may be that they merely consist of fibres which associate the hippocampus and the lateral pallial area, and have no connection with the commissural fibres. Such fibres are found in the Mammalian brain. But Ramon y Cajal distinctly represented the fibres in question as coming from the dorsal commissure.

If these fibres really exist as he represents them, and if the suggestion which I have already made to the effect that the area beyond the hippocampus represents the neopallium of the mammalian brain is correct, it must of necessity follow that *the fibres in question are strictly homologous with the mammalian corpus callosum*. That such is the case, however, I am very loth to admit, not merely for the reason that I have never been able to detect such commissural fibres passing to the lateral pallial area, but for wider morphological reasons. There can be no doubt that no such corpus callosum exists in either the Monotremata or Marsupialia, and that therefore, presumably, the ancestors of the Mammalia had no true corpus callosum, i. e. they possessed a dorsal commissure which was *purely hippocampal*. Moreover, a study of the conditions prevailing in the Mammalian brain when the corpus callosum makes its first appearance, seems to point clearly to the conclusion that the true corpus callosum develops in response to the demand of the rapidly growing neopallium for a shorter route for its commissural fibres. Such a demand can never exist in the Reptilia, in which the neopallium is of such insignificant area; and, *a priori*, one would be extremely surprised to find a representative of the true corpus callosum in the Reptilia. Yet all these strong *a priori* objections would not be of sufficient weight to counterbalance the positive evidence for a true corpus callosum which the substantiation of Ramon y Cajal's evidence would afford. The arguments of Meyer concerning its relation to the lamina terminalis, or of other writers concerning its relation to the recessus superior and roof of the third ventricle, would be of no avail if this crucial fact were established. In the meantime the question must remain in abeyance, for Ramon y Cajal's conclusions need confirmation. His observations were made and recorded without any due



sense of the morphological importance attaching to them, because he regarded the dorsal commissure as the "corpus callosum," not having recognized the hippocampus as such. Hence the fact that the fibres have a slightly wider area of origin would mean little.

The possibility of the existence of a corpus callosum in the Reptilia in this sense has not hitherto been suggested, so far as I am aware; but it is patent that *no other form of true corpus callosum can exist in the Reptilia than this, as yet, hypothetical commissure of the lateral pallium.*

I shall have occasion to return incidentally to this point later on. At the same time I cannot too strongly insist upon the fact that, even granting the existence of these true homologues of the corpus callosum in the reptilian brain, the vast majority of the fibres of the dorsal commissure are unquestionably derived from the hippocampus, and therefore cannot be regarded as part of the true corpus callosum.

In the year 1887 Bellonci published a memoir on the cerebral commissures in the Amphibia and Reptilia\*, in which he stated that in his "*tratto superiore della commissura anteriore*" decussational fibres were intermingled with true commissural fibres. The commissure to which he thus refers is the *commissura dorsalis* or hippocampal commissure, which he regarded as part of the anterior commissure—an utterly untenable view. The existence of the decussational fibres which pass obliquely from the descending hippocampal fibres of one side to the opposite side of the brain has been since observed by many investigators, and may be readily demonstrated by the method of Weigert, especially in the Saurians. These fibres are represented in the accompanying drawing (fig. 20, *a*, p. 473), which has been made, with the aid of the camera lucida, from a coronal section of the brain of *Hydrosaurus* just in front of the *commissura ventralis*. I am utterly unable to offer any explanation of this extraordinary course for fibres obviously belonging to the fornix system: nor am I able to find in the Mammalia any fibres which can be compared with these decussating bundles. No other writer, so far as I am aware, has offered any feasible explanation of this arrangement. Ramon y Cajal represented the fibres in his figure to which I have referred above; and it may be possible—although improbable—that they may represent the continuation of the fibres which he indicates as coming from the neopallium beyond the hippocampus. In other words, *they may be pallial projection fibres*. I do not, however, place any confidence in this hypothesis, and can only mention this vague possibility in lieu of the utter lack of suggestion concerning these decussating fibres. A knowledge of the alleged existence of such fibres should impose upon investigators great caution in attempting to interpret the reptilian fornix.

It is unnecessary to write at any length regarding the commissures in the cerebral hemispheres of the Bird. A study of the process of development of the chick's brain and a comparison of the histological structure of the mesial wall of the hemisphere in the adult show that in birds a hippocampus of the chelonian type makes its appearance but never attains to large dimensions. From it a small hippocampal commissure springs, as in the reptile.

To speak of a "corpus callosum" in the bird, such as Bryce and Warrington have done even so recently as 1898 (Report of International Physiological Congress, Cambridge, 1898), is a gratuitous assumption; because the dorsal commissure is unquestionably hippocampal. The same arguments concerning this homology which I have applied to the reptilian condition might be equally appropriately employed in this case also.

\* "Sulle Commissure cerebrali anteriori degli Anfibia e dei Rettili," Mem. del. Real. Accad. del. Sci. dell' Istituto di Bologna, Ser. iv. Tom. viii. 1887.

*The Comparative Morphology of the Commissura aberrans.*

The problem of the interpretation of the cerebral commissures is, however, by no means so simple as the above account may lead one to suppose. For there is in certain Reptiles the additional commissure, which I have distinguished by the name "*aberrans*." So far as I am aware, Rabl-Rückhard \* was the first writer to call attention to it, in the brain of *Psammosaurus*. He regarded it as a rudiment of the fornix or "eine Kommissur für die Ammonshörner (Forel)." His reason for this was the fact that its fibres spread out in the ventro-caudal region of the mesial wall of the hemisphere, which he regarded as hippocampus, presumably because it occupies a position which is topographically analogous to that of the Eutherian hippocampus. Osborn wrongly condemned this interpretation, and confused the *commissura aberrans* of the Reptilia with the *commissura habenularum* in the Frog, to which he had recently given the name "*commissura superior*" †. It is, however, only just to add that Osborn made this comment before he had examined any brain possessing the aberrant commissure ‡.

According to Brill §, the first observation of the aberrant commissure must be attributed to Spitzka, who recorded its presence in *Iguana* and called it "*corpus callosum*" the year before Rabl-Rückhard described it in *Psammosaurus*.

Edinger confirmed Rabl-Rückhard's observation, and adopted his suggestion concerning its homology with the "*commissura fornicis*" ||. In this memoir he calls the *commissura dorsalis* by the name "*corpus callosum*," although, like the aberrant commissure, it springs from the area which he correctly labels "Ammonshorn."

Two years later, Honegger ¶ objected to the suggested homology of the *commissura aberrans* with the fornix, and, if I correctly understand his somewhat involved argument, he regarded it as the representative of the commissural fibres of the *tænia semicircularis* (vel terminalis).

\* Rabl-Rückhard, "Ueber das Vorkommen eines Fornixrudiments bei Reptilien," Zoolog. Anz. 1881, p. 281.

† H. F. Osborn, "The Origin of the Corpus Callosum," Morph. Jahrb., Bd. xii. p. 243.

‡ [En passant I must refer to a matter not altogether pertinent to the subject of discussion. I do so in order to prevent a confusion which constantly occurs in the literature of this part of the brain. Since the introduction of the term "*commissura superior*" by Osborn for the habenular commissure, it has attained a very wide and general recognition among comparative anatomists. The names of Osborn, Bellonci, Burckhardt, Shipley, Edinger, Ritter, Studnicka, Prenant, and Sorensen, to mention only a few of those who have employed this term, indicate how general and cosmopolitan the use of this term is. And yet, since this almost universal adoption of the term, a prolific writer on comparative neurology, who claims to be familiar with the literature relating to the reptilian brain, applies this name to the dorsal or hippocampal commissure in the Monotremata and Marsupialia, viz., Theodor Ziehen, in Jenaisch. Denkschr., 1897.

While referring to a case (that of Osborn) in which the *commissura superior* had been mistaken for part of the hippocampal commissure (c. *aberrans*), I wish to protest against the singular inappropriateness of applying this same name "*commissura superior*" to the hippocampal commissure itself, and thereby deliberately introducing an element of confusion.]

§ N. E. Brill, 'Medical Record,' March 29, 1890, pp. 343-345.

|| Ludwig Edinger, *op. cit. supra*, 1888.

¶ J. J. Honegger, "Ueber den Fornix, &c.," Recueil Zool. Suisse, tom. v., 1890.



In 1892, Adolf Meyer described the commissure in *Iguana* and called it "*commissura pallii posterior*" \*.

In a series of memoirs published in 1892 and 1893, Herrick † records the presence of the aberrant commissure in a series of Lacertilian and, if I understand him aright ‡, Ophidian brains, and adopts the same view as Edinger.

In a later memoir Rabl-Rückhard ("Einiger über das Gehirn der Riesenschlange," Zeitschr. f. wiss. Zoologie, Bd. lviii.) adopted Meyer's title "*commissura pallii posterior*," and agreed with him as to its presence in Saurians only. Thus he found it in *Psammosaurus*, *Lacerta*, *Iguana*, *Podinema*, and *Chameleo*, but not in any representative of the Chelonia, Crocodilia, or Ophidia. Herrick, on the contrary, somewhat vaguely intimated that it is present in the Ophidian brain ("Topography and Histology of the Brain of certain Reptiles," Journal of Comparative Neurology, vol. iii. 1893). He referred to the *commissura aberrans* as the "hippocampal commissure," but when he added that "this does not differ in any morphological respect from the corresponding body in mammals" (*op. cit.* p. 89), it becomes clear that he had utterly failed to appreciate the extraordinarily peculiar features of this commissure.

In his latest account (1896) of the *commissura aberrans*, Edinger, who adopted the term "*commissura pallii posterior*," committed a number of errors, which are very surprising when it is remembered that he had then made a series of accurate observations on this region of the forebrain for eight years. Thus in referring to this (with the other commissures) he made the general statement "in der Lamina terminalis verlaufen die Commissuren" (*op. cit.* 1896, p. 339), without any qualification or any remark to indicate that the *commissura aberrans* does not lie in the lamina terminalis, but upon the epithelial roof of the third ventricle. This statement, moreover, was not due to a mere looseness of expression or *lapsus calami*, because in his illustration of the mesial surface of the brain of *Varanus* (fig. 4, p. 337) he represented the doubtful commissure as being attached to the upper extremity of the lamina terminalis. [This is shown even more clearly in the reproduction of the same figure in his 'Vorlesungen,' 1896, fig. 76, p. 120.]

In the text of his memoir upon the forebrain of Reptiles (*op. cit.* 1896) he makes a statement concerning the position of the *commissura aberrans* to the effect that "die caudale Mantelcommissur [*commissura pallii posterior*] liegt direkt von der Stelle, wo die Hirnwand sich zum Plexus verdünnt, wie ich das schon in meinen ersten Mittheilungen gezeichnet habe" (p. 372). This statement is in accord with the above-quoted remarks concerning its relation to the lamina terminalis and is unquestionably erroneous, because the commissure is placed *behind*, and not in front of, the situation of the mesial attachment of the lateral choroid plexus. This relationship is one of its most significant features.

\* A. Meyer, Zeitschr. f. wiss. Zool. Bd. lv. (1892) p. 63.

† C. L. Herrick, "Topography and Histology of the Brain of certain Reptiles," Journ. Comp. Neurology, 1893.

‡ Journ. Comp. Neur., 1892, p. 179.

This peculiar commissure has a very restricted distribution in the Vertebrate series. It is not found in the Chelonia nor in the Crocodilia, but seems to occur in all the Lacertilia (and perhaps in some Ophidia, although further investigations are needed to harmonize the conflicting statements of Edinger, Herrick, and Rabl-Rückhard upon this point \*). There is no corresponding commissure in the Mammalia, nor is there any exactly analogous arrangement elsewhere in the Vertebrate series. As the term "*commissura pallii posterior*" is in many respects misleading and inappropriate, as I shall have occasion to point out later on, I have introduced the name *commissura aberrans* in reference to its peculiarly aberrant nature and limited distribution.

In Dendy's otherwise excellent figure representing this commissure (fig. 15) the latter has been erroneously represented as having a complete epithelial sheath. I have represented its actual relation to the roof of the forebrain in fig. 2 (p. 457) of this memoir.

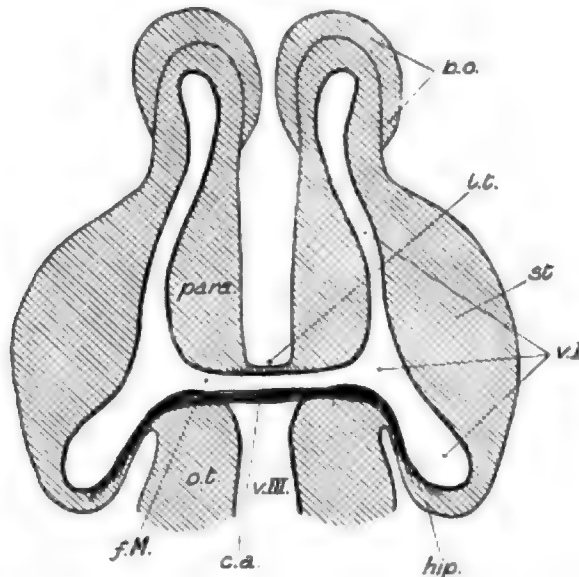
No stronger testimony of the failure to understand the meaning of this commissure could be adduced than the fact that Edinger, who has contributed a not insignificant share to our knowledge of the *commissura aberrans*, should make such fundamental errors regarding its position as I have mentioned above. But such statements are typical of the obscurity which invests this peculiar feature of the Saurian brain; and it becomes necessary therefore, in consideration of the foregoing analytical paragraphs, to reconsider the whole question of the possible significance of this commissure, because the literature of the subject affords no sufficiently well-founded clue to its nature to be of any serious value.

In the preliminary study of the roof of the forebrain in *Sphenodon*, which served as an introduction to this account, it was clearly demonstrated (*vide* figs. 1 and 2) that the *commissura aberrans* had no connection with the lamina terminalis, but is placed in a fold of the epithelial roof which is separated from the lamina terminalis not only by the lamina chorioidea (the fold from which the lateral choroid plexuses are derived) but also by the paraphysis. The *commissura aberrans*, moreover, is situated caudad of the foramen of Monro, and it marks (as I have already shown in the introduction) the line of demarcation between the strictly thalamic portion of the roof and the more cephalic region which is closely related to the cerebral hemisphere. It is therefore situated at a most important morphological site, the exact location of which may be more readily appreciated from a schematic plan of the forebrain such as the accompanying diagram (fig. 21). In this scheme the mesial cavity or third ventricle will be seen to extend forward as far as the lamina terminalis, and then to communicate by means of the foramen of Monro on each side with the lateral ventricle. The lateral walls of the third ventricle in this diagram are formed by the optic thalami, and the anterior extremity of each thalamus is joined by an attenuated band to the thin free cortical fold which forms the *labium caudale* of the cerebral hemisphere. This cortical fold is the hippocampus. From it fornix-fibres arise and proceed towards the dorsal surface of the cephalic

\* Edinger and Rabl-Rückhard are inclined to regard it as being absent in Snakes. I have been unable to find any trace of it in the Australian Snake *Pseudochia*.

extremity of the optic thalamus by the most direct route, which happens to be situated in the posterior wall of the foramen of Monro. These fornix-fibres then proceed across the roof of the forebrain and form the *commissura aberrans*. A study of the accompanying scheme will show that the commissure is placed at the exact situation in which the narrow epithelial roof of the slit-like third ventricle passes into continuity with the broad roof of the "aula," which expands in the lateral direction on each side to form the choroid plexus. The latter passes through the foramen of Monro into the lateral ventricle.

Fig. 21.



Schematic representation of a horizontal plan of the brain to indicate the situation of the *commissura aberrans*.

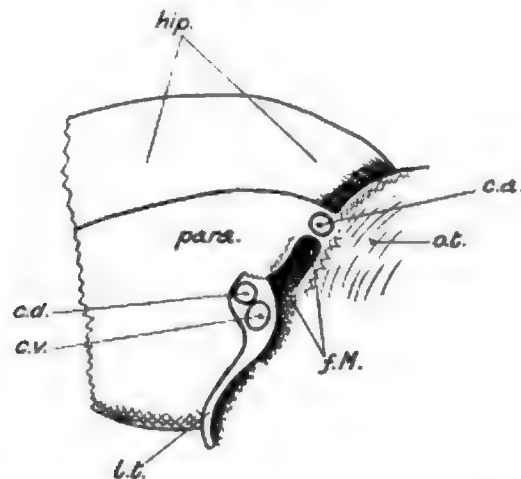
In the introductory remarks I called attention to the fact that the paraterminal body is not limited by the lamina terminalis; and I showed, by the help of drawings of coronal sections, that a process or caudal prolongation of the paraterminal body proceeds backward above the foramen of Monro, and fuses with the dorso-cephalic angle of the optic thalamus. In order to make these difficult and very complicated relations intelligible, I have constructed a crude diagram (fig. 22, p. 488) of the mesial surface of the forebrain (in part only) from which all epithelial folds have been removed.

This scheme will explain how the paraterminal body extends backward above the lamina terminalis and above the foramen of Monro, and how this caudal prolongation fuses with the optic thalamus. At the same time the paraterminal body affords a matrix or "commissure-bed" for the *commissura aberrans* just as it does for the *commissura dorsalis* and *commissura centralis*. It was to this caudal extension of the paraterminal body that Edinger gave the name "*Fornixleiste*." Other writers called it the "fornix-body" or even the "fornix." The latter term has been so used because

this part of the paraterminal body presents a relationship to the hippocampus which is analogous (topographically) to the fimbria in the Mammalian brain.

That the *commissura aberrans* arises from the hippocampus is an undoubted fact; for, as one of the coronal sections (fig. 10) in the introductory part of this memoir shows, its relationship to the caudal portion of the hippocampus is exactly analogous to that of the dorsal commissure to the same formation further forward. Therefore Rabl-Rückhard had some justification for calling this structure the *commissura fornicis*, especially as it springs from that portion of the hippocampus which persists in the Eutherian brain. But this name is objectionable, in that the designation "*fornicis*" is equally applicable to the commissural fibres which spring from the cephalic portion of the hippocampus and from the *commissura dorsalis*. Moreover, this commissure has a peculiarly aberrant course—in comparison with the usual course of the fornix—and hence it deserves a special name. The term "*commissura aberrans [hippocampi]*" seemed to me to fulfil these requirements.

Fig. 22.



This is diagrammatic, the relations of the various parts not being drawn to scale. The true proportions are shown in figs. 1 and 2, and the series of coronal sections of *Sphenodon*.

The explanation of the peculiar caudal extension of the paraterminal body is a matter of extreme difficulty, and one which needs a much fuller knowledge of its behaviour in certain other Vertebrate types than I at present possess. The question is complicated by the fact that this caudal extension seems in some way to be associated with the presence of the *commissura aberrans*. So far as I am aware, it occurs in all Reptilian brains in which the latter commissure is found, and is lacking in the Chelonia and other Reptiles in which the aberrant commissure is not developed. One might be led to believe that the *commissura aberrans* is merely a part of the *commissura dorsalis* (for both are hippocampal) which had in some way become separated from the parent commissure and in its wandering caudalward had drawn back on each side a prolongation of its matrix of paraterminal body. But the features of the region in the adult render such an

explanation improbable, nor does the history of its development in *Sphenodon* lend any support whatever to such an hypothesis. This explanation would also involve the necessity of believing that its fusion with the dorso-anterior extremity of the optic thalamus is secondary and acquired, and not the persistence of a more primitive condition. Certain other aspects of the problem will be discussed later.

But in the meantime there are certain facts which must be kept in mind in attempting to explain this phenomenon.

The paraterminal body is a ganglionic mass interposed between the *bulbus olfactorius* on the one hand and the hippocampus on the other. The only fibre-tracts which establish any connections with it are derived from these two sources. (For the sake of simplicity I do not specifically mention the connection with the cortex of the *tuberculum olfactorium*, which is merely an indirect path from the olfactory bulb.)

The morphological relations of the hippocampus and paraterminal body are thus most intimate; the latter not only affords a path for the fibres (fornix) of the former, but it forms the bond of union of the hippocampus with the olfactory region of the brain, of which physiologically the hippocampus is merely an appendage. Not only so, but a study of the relations of the *primordium hippocampi* to the paraterminal body in the Ichthyopsida lends support to the view that the hippocampus may be merely the specialized upper part of the primitive paraterminal body.

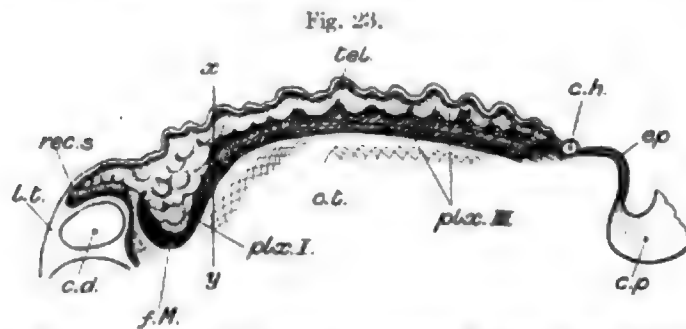
Whether this be so or not, there can be no doubt that the most intimate relationship exists between the two bodies, and any system of subdividing the cerebral hemisphere which separates hippocampus and paraterminal body commits a fundamental error which must render it nugatory as a natural subdivision.

The evidence afforded by comparative anatomy in the Vertebrate series points to the region upon the dorsal margin of the paraterminal body as the original site of the hippocampus, and it is conceivable that, as in the process of evolution the hippocampus grows backward with the hemisphere it may, in certain cases, carry with it an extension of the associated paraterminal body.

The attempt to offer an explanation of the significance of the *commissura aberrans* will involve the discussion of some of the most difficult problems in the whole field of cerebral morphology. For, before it is possible to appreciate the factors which seem to have determined the development of this commissure in the place where it is found, it will be necessary to consider briefly the involved questions: (i) of the relationship of the optic thalamus to the cerebral hemisphere; and (ii) the nature of the choroid plexus of the lateral ventricle.

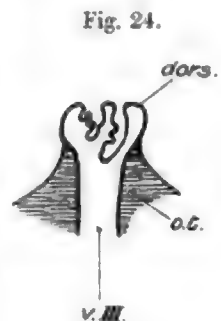
I shall discuss the second problem first, and that in relation to the Monotreme brain, because, while the latter presents all the simplicity of the Sauropsidian condition, the neighbouring regions have attained to the full degree of Mammalian differentiation, wherefore it is possible to recognize them with certainty.

The epithelial roof of the forebrain extends in *Echidna* (as in *Ornithorhynchus*, *vide supra*) from the *commissura superior* posteriorly to the antero-superior lip of the thickened upper extremity of the lamina terminalis (see fig. 23). The relations of this roof in the region of the *recessus superior* have already been considered.

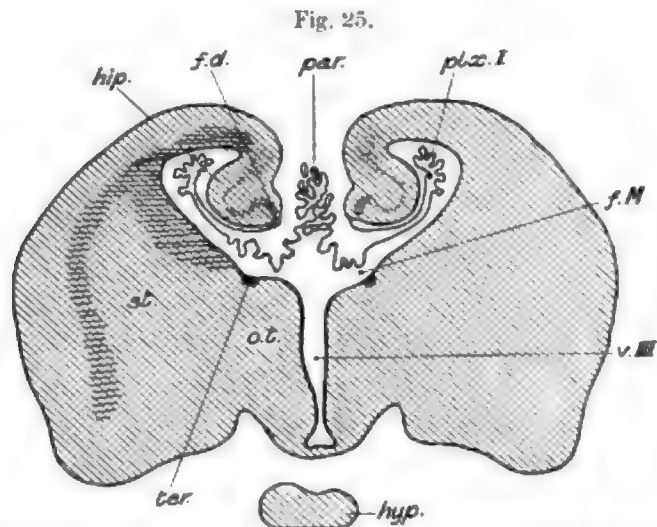


Semi-schematic representation of the roof of the forebrain of *Echidna* viewed in sagittal section.

The relations of that portion of the roof which intervenes between the *commissura superior* and the line *x-y* (fig. 23) conform to the usual plan, being attached on each side to the *tænia thalami*. The accompanying crude scheme indicates this usual mode of attachment (fig. 24).



Behind the *commissura dorsalis* a large complex fold of the epithelial roof extends on each side through the foramen of Monro to form the choroid plexus of the lateral ventricle. If a coronal section be made through the situation of the foramen of Monro, the exact arrangement of this fold will be intelligible (fig. 25) \*.



Coronal section of the brain of a foetal *Echidna*,  $\times 20$ , passing through the foramen of Monro.

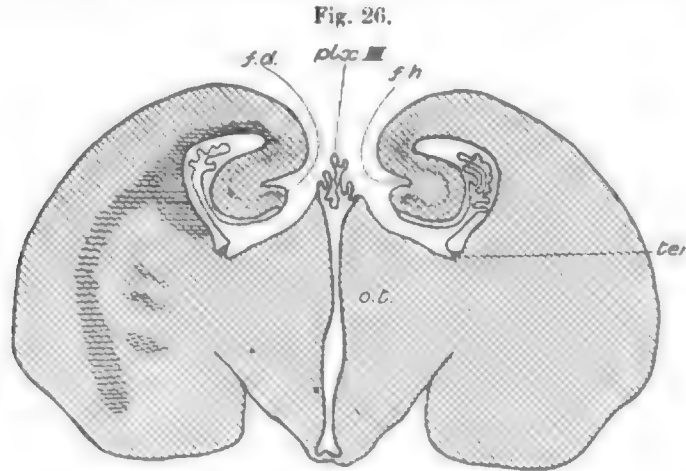
In the mesial plane it is thrown into a complicated series of folds, which form the walls of the paraphysis, and on each side the epithelial fold, forming the roof of the foramen of Monro, projects into the lateral ventricle, and is complexly plicated to form the

\* I have represented a section of a foetal brain, because it is well-nigh impossible to keep these delicate epithelial folds intact in the adult.



characteristic choroid plexus. The distal attachment of this fold is to the ventral lip of the fascia dentata.

If, however, a section (fig. 26) be made behind the situation marked *x-y* in the figure representing the roof (fig. 23), the typical thalamic roof is found to have no connection with the lateral plexus. The dorsal attachment of the latter is still to the margin of the fascia dentata, while its ventral extremity is inserted into the "*tænia chorioidea*" (His),



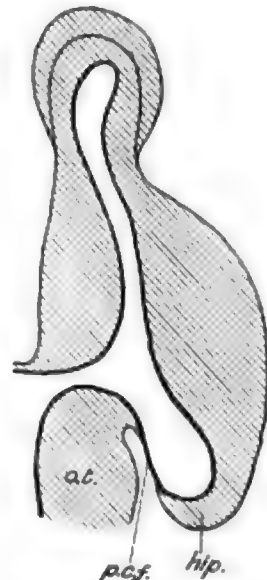
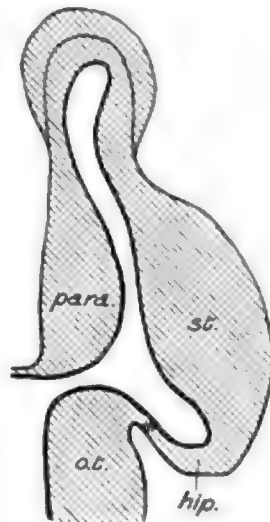
Section passing behind the foramen of Monro.

*i. e.* the stria terminalis. In the whole of the caudal extent of the ventricle the choroid plexus presents similar attachments to the margin of the fascia dentata and the stria terminalis (fig. 26).

Fig. 27.

Fig. 28.

Fig. 27 shows the primitive relation of the optic thalamus to the posterior lip of the cerebral hemisphere. The backward extension of the hemisphere will stretch the attachment to the optic thalamus at \*, and reduce it to the condition of a thin epithelial lamina as in the next figure.



Schemata to explain how the posterior choroidal fold may arise.

Now, although in the whole of its extent the epithelial layer of the choroid plexus presents uniform features, it is difficult to admit a common origin for the whole



structure. With regard to that part of the plexus which is found in the region of the foramen of Monro, there can be little doubt of its origin from the primitive roof of the forebrain. Its developmental history clearly shows that this part of the choroid plexus was never anything else than a simple epithelial layer, and a comparative study of its behaviour in different Vertebrates indicates that it ought to be regarded as a derivative of the primitive roof, or "*Deckplatte*," of the forebrain. To speak of it as a portion of the cerebral hemisphere which has undergone a retrograde change, or has retained its primitive epithelial simplicity, is to make a gratuitous assumption, which receives no confirmation from the facts of embryology. But the case is very different with that portion of the choroid plexus which is not directly connected with the roof of the forebrain, but is attached to the stria terminalis. There is no evidence to show that this portion is derived from the roof, and all the facts of development point to the conclusion that its proximal attachment to the optic thalamus is a primitive and not a secondarily acquired relation. Such being the case, the caudal extension of the epithelial choroidal fold in the Mammalian hemisphere would appear to be derived from a stretching of the attachment of the *labium caudale* of the cerebral hemisphere to the optic thalamus. As a result of this the connecting band becomes reduced to an epithelial lamina, which becomes invaginated and folded by an extension backward of the choroidal folding which begins farther forward in the region of the foramen of Monro. This hypothetical explanation of the derivation of the posterior choroidal fold is graphically demonstrated in the accompanying schemata (figs. 27 & 28, p. 491).

No full history of the mode of development of the lateral choroid plexus has ever been given, so far as I am aware. Most recent writers admit the undoubted origin of its cephalic part from the roof, and either ignore the more caudal portion or frankly admit their ignorance of its morphogenesis. The hypothesis which I have suggested to explain the possible mode of production of its caudal portion receives some support from comparative studies, and is advanced on the present occasion because the examination of the plexus in *Sphenodon* seems to have an important bearing upon the question at issue.

In *Sphenodon* the two attenuated portions of the mesial wall of the hemisphere—using this expression in its usual but inexact sense—are separated the one from the other by the *commissura aberrans*. At the situation of the latter the ventral margin of the paraterminal body becomes linked to the corresponding part of the other hemisphere, and thus a bridge is formed which effectually limits the choroidal fold. Behind the situation of this commissure the process of attenuation of the connecting band between the hemisphere and thalamus may be readily recognized. It is not difficult to conceive how, in a brain such as that of a Mammal in which there is no barrier in the shape of a *commissura aberrans*, the epithelial invagination which begins in the region of the "porta" (foramen of Monro) may extend in the caudal direction and involve the thin portion of the mesial wall of the hemisphere, which has a different mode of origin. This hypothesis might explain the peculiar attachments of the post-portal part of the choroid plexus.

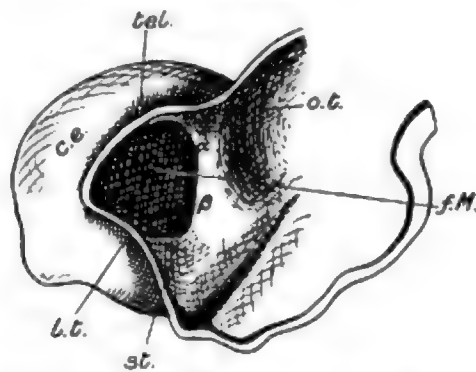
The existence in the brain of *Sphenodon* of a thin mesial hemisphere-wall, which has undoubtedly become attenuated secondarily and forms a part of the true wall of the hemisphere-vesicle linking the caudal part of the hippocampus to the optic thalamus,

naturally suggests the possibility that the caudal or post-portal part of the choroidal fold in the Mammal, which also links the hippocampus to the optic thalamus (fig. 27), may have arisen in a similar manner.

The relations of the optic thalamus to the cerebral hemisphere have been elucidated within recent years by the researches of His, Lachi, and Hochstetter. I wish briefly to call attention here to certain features in this relationship which these writers have not emphasized, and which afford the probable explanation of the presence of the *commissura aberrans* in such a peculiar locality.

From the accompanying rough sketch, which is slightly modified from one of His's drawings\*, it will be conceivable that the optic thalamus extending forward as the

Fig. 29.



Rough sketch of a mesial view of the forebrain of a human embryo of 10·2 mm. neck-length.  
Mainly after His.

lateral wall of the third ventricle, becomes directly continuous on the ventral side with the corpus striatum at  $\beta$ , whereas its dorsal part becomes continuous at  $\alpha$ , not with the ganglionic mass, but with the mantle (using this term in the original sense of Reichert).

The corpus striatum in the floor of the hemisphere may be seen extending through the widely open foramen of Monro at  $\beta$  to fuse with the lower part of the optic thalamus. But this figure is introduced more especially to demonstrate the relationship which exists between the dorsal portion of the optic thalamus and the mantle of the hemisphere at  $\alpha$ . The significance of this relationship will be understood when it is remembered that it is this "parathalamic" area of the mantle which becomes modified to form the caudal portion of the hippocampus, and that it is the connecting band between the hippocampus and the thalamus which becomes attenuated (according to the hypothesis advanced earlier in this account) and is then converted into the caudal part of the lateral choroid plexus.

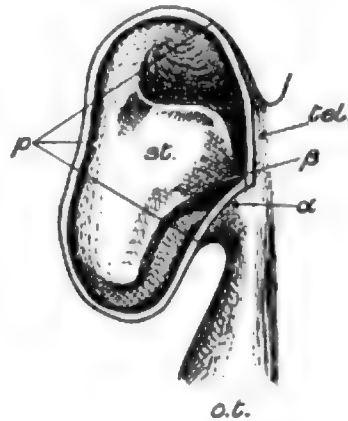
Bearing in mind these primitive relations of the thalamus to the cerebral hemisphere, which obtain at some epoch in the development of all Vertebrates and persist into adult life in the Ichthyopsida, the course of the fibres of the *commissura aberrans* becomes intelligible. For it springs from the parathalamic mantle, which becomes the hippo-

\* "Formentwick. des Menschl. Vorderhirns," Abhandl. d. königl. Sachs. Gesell. d. Wissensch., Bd. xv. No. viii. 1889.

campus at a time before the attenuation of the hippocampo-thalamic band has begun, and when, therefore, there is a close connection between not only the hippocampus and the thalamus, but also the roof of the forebrain and both of these structures.

That commissural fibres of the hippocampus should avail themselves of this direct path across the roof of the forebrain is what one would naturally expect. The puzzling feature of the problem is that the corresponding fibres in the Chelonia and Crocodilia do not make use of this route, but pursue the more circuitous path *via* the dorsal commissure.

Fig. 30.



Sketch of the dorsal aspect of the left half of the forebrain of a human foetus, drawn from His's fig. 7, Taf. i. (*loc. cit.*), with certain modifications suggested by Hochstetter's researches ('Zur Entwick. d. Gehirns,' 1898).

Roof of cerebral hemisphere dissected away.

Summing up the conclusions of the foregoing arguments, it seems that the *commissura aberrans* is a bundle of fibres derived from the caudal portion of the hippocampus, and therefore homologous (in part) with the psalterium of the Mammalia. But its behaviour presents a marked contrast to that of the Mammalia: for, instead of pursuing an extensive forward course to cross over in the lamina terminalis, it avails itself of the primitive direct connection between the caudal lip of the cerebral hemisphere and the optic thalamus, and in this way reaches the roof of the third ventricle directly. This commissure is found only in *Sphenodon* and the Lacertilia (and possibly in certain Ophidia) as a separate bundle. From examination of the brain in a number of Amphibia and related forms, it seems certain that an analogous commissure is found there also, but that instead of pursuing an independent course it crosses the roof of the third ventricle alongside the fibres of the *commissura superior* of Osborn. This phenomenon is readily understood when it is remembered that the thalamic region is very short in the Ichthyopsida, and the situations of the *commissura aberrans* and *commissura superior* would be closely approximated. The fact that the so-called *commissura superior* of Amphibia derives fibres from the caudal extremity of the cerebral hemisphere is well known, and has been recorded by almost all writers upon the Amphibian brain, so that it is unnecessary for me to adduce evidence to prove this matter of common knowledge.

But in the light of the above recorded observations upon the *commissura aberrans*, it seems more than probable that these hemispherical fibres of the *commissura superior* in the Ichthyopsida represent the aberrant hippocampal commissure of the Lacertilia and Rhynchocephalia, and do not strictly belong to the habenular or superior commissure. This interesting fact explains the otherwise inexplicable confusion of *commissura superior* and *commissura aberrans* in the mind of Osborn (Morph. Jahrb., Bd. xii. pt. i.).

Up to this point I have altogether refrained from speaking of the conditions which prevail in the Ichthyopsida, because the crucial problems with which this essay is more especially concerned find their readiest solution in the study of the Amniota. For, once a trustworthy basis for comparison of the Sauropsida and Mammalia is established, and the factors which are at play in the specialization of the various types, which Reptiles, Birds, and Mammals afford, are appreciated, the key to the solution of the problems of Ichthyopsidan morphology is provided. The comparison of a simple reptilian brain, such as the Chelonian type with the Amphibian, is a much simpler and more obvious process than the comparison of the reptilian brain with that, say, of a placental mammal.

In the Amphibia all gradations of brain-form are found, from a type which is practically identical with that of *Protopterus* or *Lepidosiren*, and differs relatively slightly from that of *Ammocetes*, up to a form which readily admits of comparison with the Chelonian type.

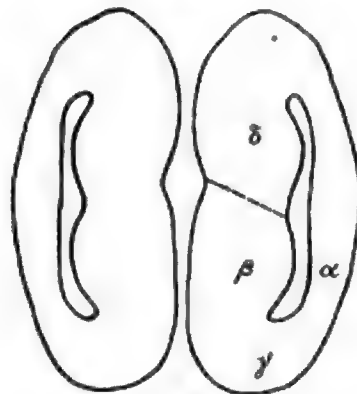
It is quite unnecessary to enter here into any long account of the features of the Ichthyopsidan types of cerebral hemisphere. So much has been written upon this subject within recent years, and the present state of knowledge has so recently been succinctly stated by Gaupp ('Anat. d. Frosches,' 1897) and Johnston (Journ. Comp. Neurol. 1900, 1901, and 1902) among many others, that the general facts concerning these types are now matters of common knowledge. But the question of the interpretation of this huge collection of facts is a very different matter, and the utmost confusion reigns in the field of Ichthyopsidan neurology. It will be sufficient, therefore, if I indicate, in the light of the conclusions drawn from the comparison of Sauropsida and Mammalia, the main sources of fallacy in the current interpretations of the Ichthyopsidan cerebral hemisphere, and point out what seems to me the true basis for accurate comparison with higher forms.

In the history of the growth of anatomical science, more especially as regards the Vertebrata, it so happens that most of the names of the various organs and of the subsidiary parts of the body were originally bestowed upon the human subject: later on these names have been applied with more or less accuracy to those parts in other animals which correspond, or are supposed to correspond, to the structures so-named in the human body. In the case of the brain, for example, comparisons were naturally made with the corresponding organ in other Mammals, and applied with doubtful results to Reptiles and Birds. In the case of the Amphibia, the data which were available for the accurate application of the terms of Human Anatomy have of necessity filtered through the uncertain channels of the lowlier Mammalian and Sauropsidan neurological knowledge, and in the process have become tainted and vitiated with all the inaccuracies which I have already exposed in speaking of the reptilian brain. Added to all the inaccuracy which necessarily results from such a process, there is the further fertile source of error which results from futile attempts at the comparison of the Reptile and Amphibian. Under such circumstances, it is no matter for surprise to find the present state of knowledge concerning the morphology of the brain in the Amphibia almost chaotic.

One example may suffice to show that this latter remark is no mere figure of speech in regard to recent work in this particular field of research.

One of the most recent writers upon the brain in the Amphibia (Pedro Ramon y Cajal, "L'Encéphale des Amphibiens," *Bibliographie Anatomique*, T. iv. 1896, p. 234) described as *basal ganglion* the lower half of the lateral (fig. 31,  $\alpha$ ) and mesial ( $\beta$ ) walls together with the connecting band ( $\gamma$ ) which forms the basal angle of the hemisphere in the Frog's brain (in a coronal section in front of the lamina terminalis). The dorsal half of the mesial wall ( $\delta$ ) he called "*septum*," meaning to imply that it is the homologue of the "*septum lucidum*" of Human Anatomy.

Fig. 31.



A still more recent writer (Ernst Gaupp, 'Ecker's und Wiedersheim's Anatomie des Frosches,' 2nd part, erste Hälfte, 1897) described as "*basal ganglion*" only that part of Ramon y Cajal's so-called ganglion which forms part of the lateral wall ( $\alpha$ ); and the mesial portion ( $\beta$ ) he called "*septum*." To complicate matters further, Ramon's "*septum*" ( $\delta$ ) Gaupp described as "*Ammonshorn*," i. e. hippocampus. Thus the only point upon which these two writers were in agreement is that the lower half of the lateral wall ( $\alpha$ ) is "*basal ganglion*." The brain of the Dipnoi is admittedly distinctly Amphibian, and as regards the cerebral hemisphere the resemblance is very striking. It is interesting to note that in *Protopterus* Rudolf Burckhardt ('Das Centralnervensystem von *Protopterus annectens*,' Berlin, 1892) regarded the upper part of the mesial wall of the hemisphere ( $\delta$ ) (Gaupp's "*hippocampus*" and Ramon's "*septum*") as the "*basal ganglion*" (vide Burckhardt, *op. cit.*, Taf. 3. figs. 22 & 23). The "*Ammonshorn*," or hippocampus, he located at the base of the hemisphere, where Ramon placed the "*basal ganglion*" and Gaupp the "*septum*" and "*basal ganglion*" (vide Taf. 3. figs. 20 & 21). Ramon (who in his most recent contribution (*op. cit.*) contradicted himself upon several occasions) added to the intricacy of the present tangle by calling the mesial portion of his "*basal ganglion*," i. e. Gaupp's "*septum*," the *epistriatum* ( $\beta$ ). The reason given by Ramon for this use of the latter term is that the region  $\beta$  corresponds to the area so-named in reptiles by Edinger. The enormity of the error involved in this amazing statement will be appreciated, when I mention that the name "*epistriatum*" was applied by Edinger to a portion of the *lateral* wall of the hemisphere in reptiles which is situated immediately *above* the true basal ganglion. The structure in question is the ventral part of the "*pallium*." It is inconceivable how Ramon can see in the lower portion of the *mesial* wall, moreover, in a region which he himself calls "*basal ganglion*," a homologue of Edinger's *epistriatum*. In the same memoir Ramon y Cajal describes as the homologue of the hippocampus the same region which he called "*septum*" elsewhere.

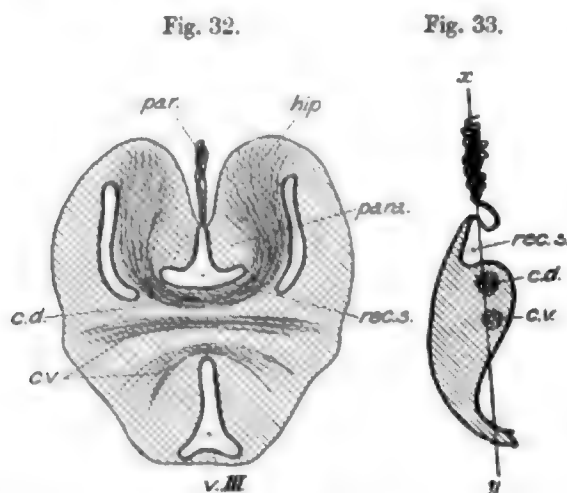
It would be possible to multiply examples almost without limit to show that even at the present time the problems of the morphology of the cerebral hemisphere in the Amphibia are in the apparently hopeless state of confusion, of which this single striking instance is unfortunately typical.

In view of the above statements it would clearly be mere waste of energy seriously to discuss further

the views of Ramon y Cajal and Burckhardt upon the morphological aspect of the Amphibian brain, for their conclusions are obviously a tissue of guesswork.

The account which Gaupp, profiting by the blunders of his predecessors, has been able to give is clearly based upon the latest memoir of Edinger (*op. cit.* 1896) upon the forebrain of reptiles, which I have discussed in an earlier part of this memoir. It is only natural under such circumstances that Gaupp's conclusions regarding the Amphibian hemisphere are marred by the same errors, which I have already exposed (*vide supra*) in Edinger's memoir. But in addition Gaupp commits some additional mistakes which create great confusion. I might quote one example. The reptilian hemisphere presents a basal notch which corresponds to the *vallecula Sylvii* of the mammalian brain. Edinger calls it the *fovea limbica*. Gaupp adopts this term, but applies it to the groove which separates the *bulbus olfactorius* from the rest of the hemisphere!

A coronal section in the plane of the cerebral commissures affords perhaps the most satisfactory basis upon which to institute comparisons with other forms, and the Frog may be adopted as a type, not because it is the most suitable Amphibian for comparison, but simply because it is best known. The accompanying diagram (fig. 32) represents schematically the appearance of a coronal section through the brain of the Frog in the plane  $x-y$  of the explanatory diagram. There are two commissures—dorsal and ventral—in the lamina terminalis as in the Reptilia. The commissura dorsalis is distributed in the dorso-mesial area of the section, which consists of a mass of grey substance containing diffusely scattered nerve-cells (*hip.*). The epithelial roof of the recessus superior is attached on each side to a mass of grey substance (*para.*) through which the fibres of



Transverse section through the brain of a Frog (*Rana*) passing through the two cerebral commissures in the plane  $x-y$ , fig. 33.

the commissura dorsalis pass to reach the area labelled *hip*. The relative disposition of these various structures is so obviously identical with that which has been seen to characterize the reptilian brain that, in the absence of any reasons to the contrary, I do not hesitate to call the dorsal area the homologue of the hippocampus, its commissure the hippocampal commissure, and the mass labelled *para.* the "*paraterminal body*."

Upon histological evidence alone one would never have suggested the homology of the



dorsal mass to the hippocampus, because its cells are diffusely scattered; but upon morphological grounds the homology cannot be questioned, and the condition of the hippocampus in *Emys* and certain other *Chelonia* indicates that a compact column of cells is not a necessary feature in the primitive hippocampus.

The morphological plan of the mesial wall of the cerebral hemisphere is so constant in the higher Vertebrata, in Reptiles, Birds, Monotremes, and Marsupials, and even in the placental Mammals (though disguised by revolutionary changes associated with the advent of the corpus callosum), that this plan must be regarded as the common property of the Vertebrata. The relations of the paraterminal body to the lamina terminalis and olfactory bulb places the recognition of this body beyond question; and the mass which rests upon its upper border and exhibits traces of a cortical structure (according to Nakagawa, *Journal of Morphology*, vol. i.), unless the Amphibian type of brain conforms to some plan utterly different from that which all the Amniota possess in common, must be the hippocampus.

Osborn and all writers who have come after him have assumed as a postulate that the dorsal commissure and the area from which it springs are the undoubted representatives of the topographically analogous structures in the Reptile. There is no other alternative which can for a moment be entertained, and therefore the amorphous dorsal mass in the mesial wall of the Amphibian hemisphere must be regarded as unquestionably the hippocampus. The question of interpretation once settled, the enormous mass of data concerning this type of brain may be readily interpreted. Three schematic representations of coronal sections in the precommissural region (figs. 34, 35, 36) in foetal *Ornithorhynchus* (it might equally be any other Mammalian foetus—*vide* His, Retzius, Hochstetter), an adult Reptile and Amphibian, will make the general plan clear.

It is quite unnecessary, with this key to the interpretation of the Ichthyopsidan brain, to give an account of all the variations of type which this heterogeneous group of Vertebrates includes. The reader who adopts this suggestion will find ample confirmation of the constancy of the plan, which the study of the Amniota has revealed, throughout the Vertebrata. The type of brain in the Anura is fully described by Gaupp, who adopts, with some relatively slight inaccuracies, the interpretation which I have put forward here (*vide* Gaupp, *op. cit.*).

The writings of Osborn (*Morph. Jahrb.*, Bd. xii., and *Journal of Morphology*, vol. ii.), and a large number of memoirs by other American writers, of which Kingsbury's account of the brain of *Necturus* (*Journ. Comp. Neurology*, 1895) may be mentioned, as well as Burckhardt's work on *Triton* and *Ichthyophis* (*Zeitsch. f. wiss. Zool.* lii. 1891), clearly show the manner in which the type becomes simplified and more fish-like in the Urodeles, producing a condition closely resembling that found in the Dipnoi\*.

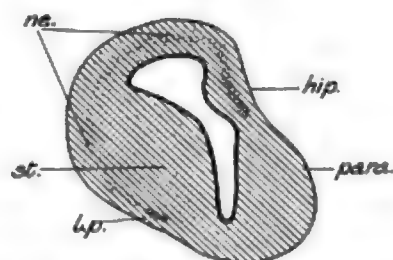
Through the kindness of Mr. E. I. Bles, of Cambridge, I have been able to study the condition of the brain in a great many genera of the Urodela, and compare them with the

\* *Vide* Fulliquet, "Recherches sur le Cerveau du *Protopterus*," *Recueil Zool. Suisse*, vol. iii. 1886; and Burckhardt, 'Das Centralnervensystem von *Protopterus*,' Berlin, 1892).



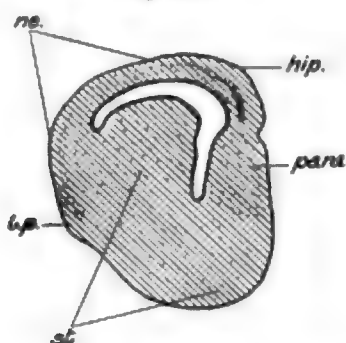
Anura and *Lepidosiren*, for the chance of examining which last I have to thank Mr. Graham Kerr. It would be impossible adequately to consider these forms here without long descriptions and a large number of figures, and it would add comparatively little to the force of the above remarks. The general plan is identical with that briefly indicated in the remarks on the Frog's brain; and if the fallacies to which I

Fig. 34.



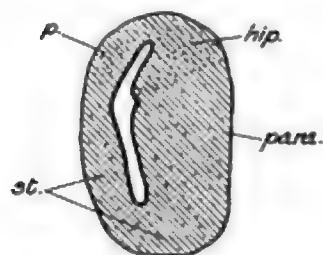
A coronal section of the cerebral hemisphere of a foetal *Ornithorhynchus* in the precommissural region.

Fig. 35.



A corresponding section—adult *Hydrosaurus*.

Fig. 36.



A corresponding section—*Rana*.

have already called attention in the works of Ramon y Cajal, Burckhardt, and to a lesser degree of Gaupp, be borne in mind, the reader can have no difficulty in interpreting aright the above-mentioned accounts of Osborn, Kingsbury, Burckhardt, and Fulliquet, and the innumerable other recent accounts of the Ichthyopsidan brain.

The vexed questions of the morphology of the piscine types of brain hardly come within the scope of this memoir. But the investigator who studies the brain of *Ammocetes* or *Petromyzon*, in the light of the information which a comparison of the Amniote and Urodele types of brain has yielded, cannot have much difficulty in seeing in the prevailing conditions in the Cyclostome an extremely simple and archaic form of the common vertebrate type. This is well shown by the important memoirs of Studnička ("Beiträge zur Anatomie und Entwicklungsgeschichte des Vorderhirns der Cranioten," Sitzungsberichte d. königl.-böhmisch. Gesells. d. Wissensch., Math.-phys. Classe, 1895) and Johnston ("The Brain of *Petromyzon*," Journ. Comp. Neurology, March 1902.).

In conclusion, I must acknowledge with the deepest gratitude the liberal help so generously afforded me by Professor Howes, who not only obtained for me the material for the research, but also devoted a vast amount of time and energy in helping me to accomplish this task.

*List of Abbreviations used in the Diagrams.*

<i>a.S.</i> , aquæductus Sylvii.	<i>o.t.</i> , thalamus opticus.
<i>alv.</i> , alveus.	<i>opt.</i> , tractus opticus.
<i>b.o.</i> , bulbus olfactorius.	<i>p.</i> , pallium.
<i>c.a.</i> , commissura aberrans.	<i>par.</i> , paraphysis.
<i>c.d.</i> , ,, dorsalis.	<i>para.</i> , corpus paraterminale.
<i>c.h.</i> , ,, habenulæ (superior).	<i>p.o.</i> , pedunculus olfactorius.
<i>c.p.</i> , ,, posterior.	<i>p.s.</i> , parietal stalk.
<i>c.v.</i> , ,, ventralis.	<i>p.c.f.</i> , posterior choroidal fold.
<i>c.f.</i> , columna fornicis.	<i>plx.I.</i> , plexus chorioideus lateralis.
<i>ce.</i> , cerebral hemisphere.	<i>plx.II.</i> , lamina chorioidea.
<i>cbl.</i> , cerebellum.	<i>plx.III.</i> , plexus chorioideus ventric. tertii.
<i>dors.</i> , dorsal sac (part of epithelial roof of the third ventricle).	<i>plx.IV.</i> , ,, ,, ,, quarti.
<i>ep.</i> , epiphysis.	<i>q.</i> , corpora quadrigemina.
<i>fasc.</i> , fasciculus marginalis.	<i>rec.i.</i> , recessus intercommissuralis.
<i>f.d.</i> , fascia dentata.	<i>rec.s.</i> , recessus superior.
<i>f.h.</i> , fissura hippocampi.	<i>ret.</i> , retina.
<i>f.M.</i> , foramen Monroi.	<i>s.l.</i> , sulcus limitans.
<i>hip.</i> , hippocampus.	<i>s.gr.</i> , stratum granulosum fasciæ dentatæ.
<i>hyp.</i> , hypophysis.	<i>st.</i> , corpus striatum.
<i>lp.</i> , lobus pyriformis.	<i>ter.</i> , atria terminalis.
<i>lt.</i> , lamina terminalis.	<i>tel.</i> , tela, or epithelial roof.
<i>mam.</i> , corpus mammillare.	<i>t.o.</i> , tuberculum olfactorium.
<i>m.o.</i> , medulla oblongata.	<i>tub.</i> , tuber cinereum.
<i>ne.</i> , neopallium.	<i>v.I.</i> , ventriculus lateralis.
<i>n.o.</i> , nervus olfactorius.	<i>v.III.</i> , ,, tertius.
<i>n.IV.</i> , nervus trochlearis.	<i>v.IV.</i> , ,, quartus.

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## ERRATA.

- Page 68, lines 15 and 16 from top, for *ACHROSA SCHREIBERSII*, Perty, read *ACHROSA SCHREIBERSII*, Perty.  
 Page 71, line 2 from bottom, for *Sympetrum gilvum* read *Sympetrum gilvum*.  
 Page 89, line 3 from bottom, for *Memoirs of the Acad. of Vienna*, 1852, vol. iii., read *Denkschr. k. Akad. Wiss. Wien*, Bd. iv. Abt. 2 (1852).  
 Page 101, line 10 from top, for *Armadillo regulosus* (= *Cubaris regulosus*, Miers) read *Armadillo rugulosus* (= *Cubaris rugulosus*, Miers).  
 Page 101, line 10 from top, for *Cubaris regulosus*, Miers, read *Cubaris rugulosus*, Miers.  
 Page 104, line 11 from bottom, for *Lygia* read *Ligia*.  
 Page 118, line 5 from bottom, for *Porcellis* read *Porcellio*.  
 Page 128, line 5 from bottom, for *Mesarmadillo Alluandi*, Dollfus, read *Mesarmadillo Alluandi*, Dollfus.  
 Page 167, line 10 from bottom, for *Eluropus* read *Elurus*.  
 Page 167, line 9 from bottom, for absence read presence.  
 Page 168, lines 17 and 18 from top, omit mention of *Hyænarctus*, the humerus of which is unknown.  
 Page 184, line 2 from bottom, for *Tachybaptus fluviatilis* read *Tachybaptus fluviatilis*, Tunst.  
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